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Living Attached: Aufwuchs, Fouling, Epibiosis

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Introduction

This synopsis presents an overview based on recently published work (mostly 1985 through 1994) on the biological and technical aspects of marine aufwuchs, e.g., life forms growing attached to solid/fluid interfaces (substrata) without depending trophically on their substrata. Aufwuchs encompasses the general phenomenon, while fouling and epibiosis refer to aufwuchs on nonliving and living substrata, respectively. The central theme will be the interaction between organisms and the substrata. For this reason, only sessile and hemisessile species are taken into account. Vagile organisms are not considered true aufwuchs organisms here because they have the potential for switching habitats and, therefore, are less definitively linked to the substrata. The substrata bearing aufwuchs may be extremely variable in size, consistency, chemistry, and longevity. They may be of geochemical, biological or man-made origin.

In the first section some reasons are given why attached life is a typically aquatic phenomenon and rarely encountered on land. The latter part of the section deals with the mechanisms of substratum colonization. The second section treats the subject of "fouling". This rather partial term designates the aufwuchs on nonliving substrata, which in the case of man-made, immersed structures often interferes with human interests. "Epibiosis" on the other hand (third section), describes the association of organisms growing attached to other living organisms. Here, the occurrence of epibiotic associations and epibiosis-caused biological and ecological effects are dealt with. The last section speculates about antifouling solutions as derived from epibiosis research.

many thousand species with representatives from most of the marine phyla have adopted this mode of life for at least one ontogenetic phase: many bacteria, many protozoa, many diatoms, most macroalgae, all sponges, most cnidarians, many molluscs (bivalves, gastropods), some rotifers, most bryozoans, most phoronids, many brachiopods, many tube-building polychaetes, some echinoderms, a few crustaceans (especially cirripedia), some hemichordates, all ascidians.

In many shallow, hard-bottom habitats, sessile life forms dominate the benthic community by number of individuals and species. The decoupling of feeding medium (water) and attachment medium (substratum) may make suitable settlement area a limiting factor in marine habitats. Colonization pressure is a function of locally and seasonally available colonizing species as well as physicochemical and nutritional properties of the water. While never nil, it may vary enormously seasonally and geographically: it may take months in the western Baltic winter for the first visible biofilm to show, while salmon cage netting has to be changed weekly because of heavy fouling in Tasmanian summer waters (Hodson and Burke 1994). Wahl and Lafargue (1990) introduced an index to evaluate the suitability (or rather unsuitability, defense) of a substratum for colonization.

$$\text{Antifouling Potential} = (1-E/CP) \times A/(FP+A)$$

with E = number of aufwuchs species found on a substratum, CP = numbers of species of local colonizer pool, A = longevity of the substratum, FP = time between immersion and arrival of first metazoan larvae (as an arbitrary estimate colonizing intensity). The index may be used to evaluate the unsuitability of a substratum (e.g., efficiency of antifouling paint or biological defense), but is primarily thought to illustrate the parameters controlling colonization intensity. Thus, a long lived (high A) surface exposed to intense fouling pressure (short FP, high CP) but remaining scarcely fouled (small E), may be expected to be unsuitable for settlement or well protected against colonizers.

Colonization of an Immersed Substratum

Surface Properties

"On immersing a surface in sea water, a complex process of colonization is initiated" (Davis et al. 1989). This statement, or variations of it, can be found in the introductions of most publications treating the subject. It can be, and sometimes is, phrased more sharply: "*Any* hard substratum immersed *anywhere* in the ocean will *inevitably* become colonized—if it is not continuously disturbed or well defended." This is bad news (although not really new) for the antifouling industry (see section

on fouling). The two restrictions "disturbance" and "defense" will be treated in the following sections. A closer look at the three main items of this generalization in reverse order, follows.

Inevitable Colonization: Regardless of place and substratum type, an aufwuchs community will establish. Yet, this process will vary in colonization speed, density, and species composition with latitude, depth, exposure time, season, colonizer pool, water chemistry, and substratum characteristics.

Anywhere: As suggested by the widespread occurrence of sessile species across prokaryote, animal, and plant kingdoms, it is not surprising that some potential colonizers can be found anyplace in the ocean: from the poles to the tropics, from the sea surface to hadal depths, from estuaries to offshore waters, from sewage outflows to low-nutrient gyres. Again, intensity of colonization will depend on such local parameters as temperature and nutrient availability, and species composition will be a subpopulation of the local colonizer pool.

Any Substratum: Maybe the most amazing observation of previous reports is, that any stable surface is subject to some kind of colonization. Substrata as diverse as glass, aluminum, steel, copper, titanium, sandstone, granite, slate, concrete, PVC, Teflon, Plexiglas, coral, algal surfaces, mollusc shells, crustacean carapaces, polychaete tubes, diatom valves, soft animal tissue, wood, and many more will develop aufwuchs communities—albeit often featuring only a small subpopulation of locally available colonizer species.

Usually, substratum types do not only differ by their chemical composition, but also one or more of other properties such as wettability, color, consistency, roughness, longevity, size, irradiation, inclination, orientation.

Wettability, a function of surface free energy, ranges from hydrophobic to hydrophilic. This surface property strongly influences the spreading and adhesion of the attachment glues or cements used by many settling colonizers.

The color (or grey shade) of the substratum is important for optically cueing larvae, but its importance will decrease with water depth.

The consistency of a substratum may range from steely hard to watery mucus (some algae, cnidaria) and from rigid to flexible, and should have implications especially for larger, shell secreting or rigid colonizers.

Surfaces may be anything from smooth (e.g., glass, many algae) to granular (e.g., sand stone, some carapaces), scaly (e.g., some bivalve shells), hairy (e.g., some algae and polychaetes), and so on. Microtopography of the surface may influence settlement by modulating small scale hydrodynamics or by reducing available flat area for

attachment. Although promising, the role of surface roughness in colonization processes has not yet been investigated to any extent.

The significance of substratum longevity obviously depends on the life cycle of a given colonizer species. Successful settlement and reproduction on a surface can be achieved within weeks by bacteria, diatoms or protozoa, while higher animals or algae depend on surface stability over months or even years. Substratum longevity, meaning the persistence of conditions as they are at the onset of colonization, may be delimited by abiotic changes (emersion, drastic changes in salinity, oxygen concentration, pH, etc.), by mechanical alteration of the surface (overturning of sand grains or boulders, abrasion, erosion, ablation, sloughing, etc.) or by the life expectancy of a living substratum (leaf, carapace, integument, whole organism). A successful colonizer should be able to develop and reproduce before its substratum vanishes or surface conditions become intolerable.

Appropriate size is a prerequisite for colonization. Available, reasonably flat, surface area should exceed the dimensions of the settling form (cell, larvae, spore) and, better still, the attachment area of the adult. An oyster larva will not settle on a diatom, a diatom not on a bacterium.

The remaining three parameters — irradiation, inclination, orientation — affect the substratum's exposure to light, water movement, and siltation.

As mentioned before, all undefended surfaces will be subject to some sort of colonization. The development of an aufwuchs community may be slowed down on certain substrata, the aufwuchs may be less dense or less diverse. But no combination of the above properties makes a substratum wholly unsuitable for all potential settlers. There are two reasons, at least, for this phenomenon. First, among the multitude of locally available colonizer species, there will always be some (especially among the bacteria) that can cope with a given set of surface conditions. Second, the development of aufwuchs is a multistep, selforganizing process (see next section). Many of the surface properties will be altered, neutralized or masked by the first layer(s) of pioneer colonizers, and thus become less relevant to later settlers.

Colonizing Sequence

The physical, biochemical, and biological events leading to the establishment of an aufwuchs community have been thoroughly investigated. Details can be looked up in the more general references given in this section or the literature cited in these. In the following, the sequence of events most commonly observed is outlined very roughly. While most descriptions are based on the colonization on artificial substrata (metals, glass, polymers) immersed in the sea, similar processes

have been observed in other media (freshwater, blood, saliva) and on different substrata (wood, stone, teeth, coral skeletons, living organisms). The model thus seems to be of some general value. Yet, in each particular set of conditions, variations can be expected with regard to speed of colonization, number of steps involved, species settling, etc.

The colonization of a substratum is generally viewed as a four-step process: biochemical conditioning of the surface, bacterial colonization, diatom and protozoan colonization, settlement of larvae and spores (figure 1). These steps usually set in sequentially, but the different subcommunities continue evolving throughout the life span of the substratum, interacting with each other.

Colonization pressure begins acting the instant of first contact between seawater and substratum: launching of a ship, hatching of a larvae, splitting of a boulder, appearance of new surface through sloughing of a cuticle or growth of a seagrass blade. For simplicity, this instant will be called "immersion".

Biochemical conditioning: Seawater does not only contain inorganic salts, but also a variety of organic compounds such as sugars, amino acids, proteins, lipids, a multitude of secondary metabolites, etc. Physical properties (surface free energy, polar and nonpolar components, wettability) of substratum and water are virtually never identical (Dexter 1976). The resulting thermodynamic forces across the solid/liquid interface are the motor of the adsorption of organic macromolecules (mostly glycoproteins, polysaccharides and proteoglucanes) onto the substratum. As this process (de-mixing) reduces the randomness of molecular distribution,

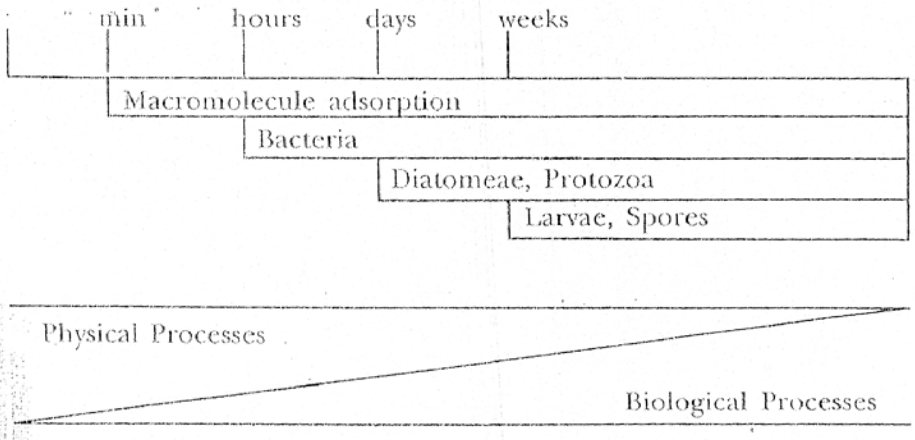

Figure 1. Schematic of colonization sequence figuring the four overlapping phases and the change of dominant forces from physical to biological (logarithmic time scale, modified after Wahl 1989).

the accompanying loss of entropy must be compensated by a diminution of the system's total free energy. This is apparently ensured by the replacement of the initially high-energy solid/liquid interface by a lower energy organic layer (Dexter 1978, Dexter and Lucas 1985). This adsorption is purely physical and spontaneous (Baier 1984). It begins within seconds to minutes after immersion. As most substrata, independently of their original surface properties adsorb similar, often amphoteric macromolecules, their surface free energy and associated wettability, usually converge toward a 30–50 mN/m range during this process (Baier 1981, Becker and Wahl 1991), with hydrophobic surfaces increasing and hydrophilic ones decreasing in wettability. Furthermore, conditioning films forming on different substrata exposed under the same conditions are similar (Little 1985). These are examples of how substratum properties may become masked during colonization (e.g., Schneider 1994). However, on substrata with initial wettability in the range 20–30 mN/m, binding strength and compactness of the conditioning film appear to be reduced (Baier 1981). A further aspect of this adsorption is that physical, chemical, and biochemical characteristics of this macromolecular film are quite different from those of the surrounding seawater. In particular, the concentration of macromolecular nutrients at the interface is thought to have an impact on subsequent colonization steps (e.g., Wardell et al. 1983).

Bacterial colonization: Beginning within hours after immersion, this phase is of mixed physical and biological nature (figure 2). While settlement of bacteria (small size, low Reynold's numbers) has been compared to that of colloid particles (e.g., Marshall 1972, Characklis 1981), bacterial behavior (motility, chemotaxis) undoubtedly contributes significantly to this process (Chet and Mitchell 1976, Mitchell and Kirchman 1984). The nature of forces involved in bacterial transport changes with distances (from the surface) considered: water currents (km, m, cm), cell motility, microturbulence, Brownian motion, gravity (mm, µm), electrostatic and Van der Waal interactions between cell and substratum, fibril contraction (µm, nm) (e.g., Characklis and Cooksey 1983). In this context it is important to realize that water layers near a surface behave physically differently from bulk water. Mostly due to friction, any surface bears an almost perfectly stationary water "skin", called the viscous layer (thickness 40–100 µm), a manifestation of the no-slip condition on every surface. Thinner still (≈ 10–20 nm) and closer to the surface, lies the electrical double layer composed of physically highly structured water molecules and dissolved ions (electrostatic interaction with the substratum).

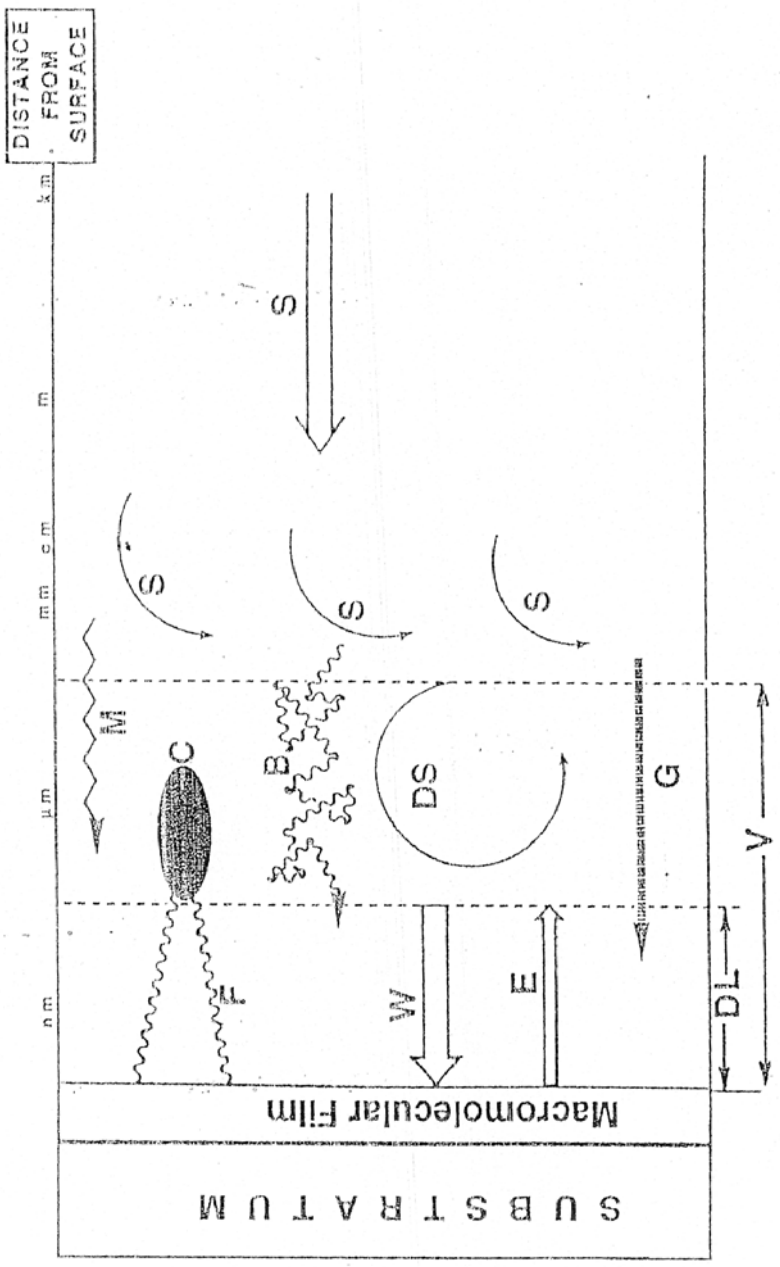

Figure 2. Forces involved during bacterial colonization as a function of distance (log-scale) from surface. B = Brownian motion, C = cell, DL = electrostatic double layer, DS = downsweeps, E = electrostatic repulsion, F = fibrils, G = gravity, M = bacterial motility, S = currents, V = viscous layer, W = Van der Waals attraction (modified Wahl 1989).

Long range transport of the cells up to the outer borders of the viscous layer will be governed by water currents mostly. Approach through the viscous layer is motored by cell motility (if present and if chemotactically attracted), by random Brownian motion or by microturbulences (downsweeps) that occasionally break through the viscous layer. Most cells and substrata are predominantly negatively charged. So, on further approach, the antagonistic forces of electrical repulsion and Van der Waal attraction between cell and substratum tend to immobilize the cell at a distance of 3–20 nm from the surface. Rearrangement of glycocalyx polymers (Schneider 1994) and/or production of fibrils, attachment of these, and subsequent enzymatic shortening (Fletcher and McEldowney 1984) may help to overcome the repulsion and pull the cell into contact with the surface. This last phase of settlement is facilitated by an opposite charge of cell and substratum, by a hydrophobic cell surface or by reduced cell diameter as in rod shaped bacteria (e.g., Absolom et al. 1983, Pringle and Fletcher 1983, Fattom and Shilo 1984). Firm attachment is achieved by covalent bonding between glycocalyx polysaccharides and binding sites on substratum or macromolecular film (often through divalent cations or lectins, e.g., Costerton et al. 1978). Subsequent, often copious production of exopolymers and continued bacterial settlement lead to the formation of a complexly structured biofilm: matrix compartments containing dead and living cells are separated and interconnected by a branching channel network in which nutrients and wastes circulate (Schneider 1994). The biofilm matrix not only serves as a mechanical support for the bacteria, but also enables these to create microhabitats suitable for their physiological demands. Within the biofilm, physicochemical conditions may locally be drastically different from bulk water with regard to solute concentrations, oxygen tension, pH, redox potential, etc. (e.g., Dexter 1993). During bacterial colonization, successional features have been suggested (e.g., Marshall et al. 1971, Corpe 1972), although in most studies bacteria are rarely identified to genus or even species level. Generally, rod-shaped bacteria seem to arrive first, followed by coccoid and, finally, stalked forms. Even during the subsequent phases of colonization, the biofilm community continues to evolve under the influence of recruitment, predation, competition, and disturbance (Little 1984).

Diatom and protozoan colonization: The settlement of eukaryote unicellulars typically begins within days to weeks after immersion of a new substratum. These cells are subjected to the same physical forces as bacteria. But due to larger cell size and higher motility (at least in the case of many ciliates), their contribution to the adsorption process relative to behavioral aspects should be smaller. After contacting the substratum,

the cells attach with polysaccharide or protein glues to biofilm, conditioning film or substratum surface (e.g., Tosteson et al. 1983, Cooksey et al. 1984). Wettability and availability of suitable linkage sites are of relevance. The most common sessile protozoa are foraminiferans or ciliates, the latter mostly of the *Folliculina, Vorticella, Zoothamnion* or *Suctoria* type. Some aufwuchs diatom genera found around the world are *Coscinodiscus, Licmophora, Asterionella, Synedra, Achnanthes, Cocconeis, Navicula, Nitzschia, Amphora*. Diatoms usually dominate this third phase of colonization, but ciliates may reach peaks during spring (personal observation in the Western Baltic) or on specific substrata (e.g., certain crustacea: e.g., Precht 1935). This aufwuchs subcommunity, too, exhibits succession (O'Neill and Wilcox 1971, Ferreira and Seeliger 1985), and dynamic evolution.

Colonization by pluricellular eukaryotes: The settlement, succession and dynamic interactions of macrofoulers (animals and algae) is undoubtedly the most extensively studied phase of the aufwuchs sequence. Some key publications on this subject comprise Sutherland (1974), Jackson (1977), Osman (1977), Sutherland and Karlson (1977), Hadfield (1986), and Richmond and Seed (1991). While succession has been thoroughly investigated, predictability remains poor (Richmond and Seed 1991), and the existence of multiple stable points seems to be rather the rule than the exception (Sutherland 1974, Law and Morton 1993). This may equally hold true for bacterial, diatom, and protozoan colonization, but has not yet been demonstrated.

One important difference to the previous settlement phases should be mentioned. Settlement is done not by the adult life form or something similar in most respects, but by a "gene vehicle" (larva, spore, etc.). Typically, the latter differs from the adult it will grow into by almost any criterion: size, motility, biology, and physiology. The adult is larger by orders of magnitude and lives, and thus depends on stable substratum, for months to years. Furthermore, distal parts of the growing organism often leave the protective proximity of the substratum chosen by the settling form to encounter conditions quite different with regard to hydrodynamics, light, nutrient supply, and the like. To meet the challenge of choosing for a different life form, the adult, many larvae (and spores?) rely on a set of settlement cues, which with evolutionarily satisfying probability, indicate the "right" attachment site. Numerous such cues have already been described, including light levels, hydrodynamics, gravity, surface texture, roughness, color and wettability, surface chemistry, presence of certain other aufwuchs organisms or conspecifics, exuded secondary metabolites, etc. (Neumann 1979, Olson 1980, Todd and Doyle 1981, Kirchman and Mitchell 1983, Crisp 1984, Morse 1984,

Rittschof et al. 1984, Burke 1986, Butman 1986, Wethey 1986, Chabot and Bourget 1986, Roberts et al. 1991, Morse 1992, Leitz and Wagner 1993). Negative cues may be as important as positive triggers. Persistent absence of positive cues may lead to a prolongation of larval phase, a lowering of the cueing threshold, metamorphosis without settlement and/or death of the larva.

While the four colonization phases described typically start sequentially, they coexist and intensely interact for the rest of the aufwuchs community's life span.

The above model is certainly a very simplified view of aufwuchs development. For a given location or season, single phases may be skipped, subsequent phases may start simultaneously or even in reverse order. But the presented sequence is by far the most commonly observed. This probably has a dual reason: availability of colonizers and facilitation:

- From macromolecules, over bacteria, diatoms and protozoa, to larvae and spores exists a decreasing gradient of presence (spatial and seasonal) and concentration in seawater. Thus, the encounter probability between newly immersed substratum and settling unit follows the same gradient. Furthermore, macromolecules and the physiologically very adaptive bacteria are less 'choosy' with regard to substratum properties than larvae, for instance.
- In addition, there are examples of facilitation in aufwuchs succession. Adsorbed macromolecules constitute a potential nutrient source for chemotactically attracted bacteria (e.g., Wardell et al. 1983). Also, the conditioning film often exhibits much less extreme surface-free energy values than the original substratum. Biofilms are known to neutralize adverse substratum properties by detoxification or masking (e.g., Saroyan 1968). Bacterial vitamin production (Lynch et al. 1979), N_2 production (Goering and Parker 1972) and provision of suitable linkage sites may facilitate subsequent colonization phases. Bacteria and diatoms may produce settlement cues for larvae (e.g., Crisp 1984, Kitamura and Hirayama 1987).

It seems reasonable that availability and facilitation concertedly constitute the causal basis for the usual sequential character of aufwuchs development.

Fouling

The rather anthropocentric term "fouling" originally described those aufwuchs communities that develop on man-made structures in the sea,

and that usually interfere with human interests. Unfortunately, this term is often extended to any hard bottom community or, at least, its attached components. There certainly is nothing foul, dirty, disgusting or putrid (Webster synonyms) about kelp forests, mussel beds or gorgonian communities. On the other hand, sessile organisms settling on underwater structures man-designed for a specific use may indeed severely interfere with this function.

As mentioned before, fouling pressure of variable intensity is omnipresent in the sea. Generally, it decreases with latitude, distance from shore, distance from natural hard bottom communities, and depth (Richmond and Seed 1991). On undefended substrata a fouling sequence corresponding to the above model can be observed. On protected surfaces; however, the sequence may be substantially altered or truncated for a limited amount of time (see below). For convenience, marine engineers distinguished between:

- microfoulers (bacteria, cyanobacteria, diatoms, protozoa),
- soft foulers (without calcareous excretions: many algae, sponges, hydrozoa, sea anemones, soft corals, polychaetes, ascidians, etc.),
- hard foulers (with calcareous excretions: calcareous algae, stony hydrozoa and corals, bivalve molluscs, bryozoans, cirriped crustaceans, polychaetes, etc.), and
- borers (representatives of cyanobacteria, sponges, isopod crustaceans, bivalves, polychaetes, sea urchins, phorinids, etc.).

All types of surfaces may become fouled, while boring is restricted to mineral materials (stone, concrete), wood and, rarely, metals (some urchins, sulfate-reducing bacteria in the last case). The unwanted effects of fouling comprise the following aspects: destruction of material, insulation, accrual of mass, and increase of frictional drag.

Effects of Fouling

The destructive potential of fouling is known since man began using wooden boats. Especially, when ships became larger and could not be dragged ashore between uses, the danger of loosing vessel (and crew) to *Teredo, Spaeroma,* and other borers increased. In areas with high borer incidence like the Indian Ocean, every single one of 60 timber species tested was destroyed by borers within 12 months (Santhakumaran and Rao 1988). Evidently, not only ship hulls are attacked, but also any other wooden material immersed in the sea: rafts, pilings, live mangrove trees, etc. (Boyle 1988, Nagabushanam and Alam 1988, Rao et al. 1991). Besides wood, other materials, too, are subject to boring. Calcareous rock

or construction blocks are a suitable substratum for diverse borers belonging to the cyanobacteria, the sponges (e.g., *Cliona* sp.), the tube worms (e.g., *Polydora* sp.), the echinoderms (e.g., *Stomopneustus* sp., *Echinometra* sp., James 1989) or the tentaculata (e.g., *Phoronis* sp.). Even concrete and steel may be bored into by some sea urchins (e.g., Patil et al. 1988, James 1989). While many borers only use the substratum as an anchoring site (e.g., *Polydora, Phoronis*) or shelter (*Cliona,* urchins), others trophically depend on this material, mostly digesting wood with the help of associated bacteria or ciliates (boring bivalves and isopods). This last group, strictly speaking, does not belong to the aufwuchs as defined above, but they certainly contribute substantially to the fouling problem.

In still another way, material degradation may be favored by fouling: corrosion in a wide sense is the deterioration of polymers, plastic, rubber, cement, wood, and metals (Aroujo-Jorge et al. 1992). When foulers, in particular bacteria, are involved in the process it is termed biocorrosion. In the case most relevant to marine engineering—steel (Coutinho et al. 1993, Dexter 1993)—atomic iron is oxidized to $Fe(OH)_2$ with either oxygen and water (aerobic conditions) or hydrogen ions (anaerobic conditions) gaining electrons from the metal (Aroujo-Jorge et al. 1992). As iron oxide is more voluminous than metallic iron, corrosion of steel embedded in concrete may provoke cracking of the latter (Patil et al. 1988). The corrosion-promoting role of foulers consists in creating favorable conditions at the metal surface (low oxygen tensions, extreme pH values, high H_2S concentrations) or by directly attacking the metal. The electrochemistry of biocorrosion is extensively treated in Aroujo-Jorge et al. (1992) and Dexter (1993).

The insulation effect of fouling impairs the functioning of immersed heat exchangers (DePalma et al. 1979), reverse osmosis membranes (Ridgway et al. 1985) and electronic or optical probes.

The accrual of (bio-)mass on marine structures has different aspects. The increase in weight due to settlement and growth of macrofoulers, in particular hard foulers, can be substantial. When occurring on floating objects such as boats, rafts, floats, moorings, etc., the weight of foulers may eventually exceed buoyancy, resulting in sinking of these objects (e.g., T. Lewis 1994). The added crust on originally flexible structures (ropes, nets, chains, cables) makes them not only heavier, but also more rigid and brittle, increasing the risk of breakage. Already moderately thick layers of macrofoulers may severely interfere with the functioning of any moving parts (rudders, fins, propellers, robot arms, hatches). A severe security problem may be the clogging of pipes in water circulation systems of vessels, offshore platforms, onshore power stations or desalination plants (Marotz 1985). Fouling of aquaculture nets increase their weight and decrease water exchange through the meshes, causing a deterioration of water quality within the cages (Hodson and Burke 1994, T. Lewis 1994). Maybe the best known fouling-caused problem is the increase of frictional drag. Even biofilms are reported to increase friction on a ship hull by 80% (Lewthwaite et al. 1984, as cited in J. Lewis 1994). Macrofouling has proportionately larger effects and may decrease operating speed and increase fuel consumption and overall costs substantially (J. Lewis 1994).

Macrofouling on structures subjected to acceleration/deceleration cycles (rhythmically moving objects or wave-exposed stationary structures) causes additional strain in a four-fold manner: deterioration of material, increase of diameter and thus drag exposed area, increase of surface friction, increase of the so-called added mass. In fact, the total in-line force acting on an object in unsteady flow is the sum of drag and accelerational force (Gaylord and Denny 1994). The former increases with surface friction. The latter depends on the mass of the object to be accelerated plus the mass of water entrapped within parts of the object, e.g., the seawater in or between branching, tuft-like macrofoulers (algae, hydrozoans, gorgonians, etc.). During acceleration this added mass water is squeezed out to a degree that depends on water velocity and flexibility of the entrapping organism.

In specific circumstances, fouling may be beneficial. Biofilms are used in chemical transformation processes and in waste-water treatment (Marshall 1994). Alkaline barnacle cyprid cement has been suggested to reduce corrosion (Patil et al. 1988).

In conclusion, fouling generally is not only unsightly (to the ship owners), but also may shorten the service expectancy of immersed structures and make their operation expensive, less dependable or even hazardous.

Costs of Fouling

The fouling-related costs to marine industry are composed of prevention (antifouling protection measures), increased operational costs, compensation (use of more resistant and usually more expensive materials, and sturdier constructions), replacement of fouling-damaged parts, restoration after fouling-caused accidents. Estimates of these costs vary greatly, depending on region, industry and detrimental effect(s) considered. Some examples of fouling induced costs, given in no particular order in table I, may illustrate the amplitude of the problem.

In view of these numbers, in particular the estimate of savings due to antifouling protection, industry's motivation to develop and employ efficient fouling-prevention methods is not surprising.

Table 1. Fouling related costs to marine industry.

Industry	Cost	Source
U.S. oil industry	16–18 bill.$/y	Aroujo-Jorge et al. 1992
Tasmanian-Atlantic Salmon	800,000 $/y	T. Lewis 1994
U.S. Navy (additional fuel)	75–100 mill.$/y	J. Lewis 1994
Cleaning of platform legs	250,000 $/y	Pearce 1994
Savings due to protection	2.449 bill.$/y	Collinson and Grant 1994

Antifouling Protection

Fouling can be kept at a tolerable minimum by periodic renewal of the surface, inducing unstable physicochemical conditions at the surface, mechanical cleaning, impeding adhesion, repelling potential settlers or intoxication. During the ages, a vast variety of these approaches have been employed with variable success.

Traditional methods

Since thousands of years, coatings are employed both for sealing (of wooden crafts) and for protection against foulers and borers. Before the birth of the modern chemical industry, natural products or simple derivatives of these were used. Tar, pitch or other bituminous materials, waxes, seed oils, lime, cashew-nut shell oil, and rubbers (Santhakumaran and Rao 1988, De 1989b, Foster 1994) have been and often still are employed. The performance of these substances depends on local fouling pressure and the specific composition of the local colonizer pool. In the very fouling-active and borer-rich waters of the Indian western coasts, they do not provide sufficient protection, and have to be combined with other methods (exposure to air, scraping; De 1989b).

Another form of coating used in historical times was the sheathing of wooden hulls in metals that liberate toxic ions during surface corrosion: lead, bronze, and copper (Foster 1994). While these performed quite well, they increased ship weight substantially, and wood deterioration beneath the metal plates was probably difficult to detect and repair.

Modern toxic coatings

The development of modern antifouling paints consisting of a matrix carrying one or more toxic compounds began in the 17th century with a composition based on arsenic, copper, and gunpowder (Foster 1994). Since then, the performance of antifouling paints (inhibition and service life) was gradually improved by new or new combinations of additives (mercury, tin, etc.), by adapting the matrix to service demands, and by regulating the leaching rate. Because the leaching from simple

additive-in-matrix suspensions is a function of the concentration difference between paint and water, leaching decreases rapidly with time, and toxic agents initially have to be severely overdosed to ensure an acceptable service life. Also, leaching rate increases, while fouling decreases, with ship speed. It also depends on salinity, temperature, presence of biofilm, etc. (Foster 1994), and certainly does not vary in harmony with fouling pressure as would be desirable. Some progress has been made, though. Types of modern antifouling compositions are described by Bowmer and Ferrari (1989) and Foster (1994). The most widely used antifouling paints are tributyltin self-polishing compositions (TBT-SPCs). In this system, organotin is covalently bound to an acrylic polymer matrix. Hydrolization of the bonding releases the antifouling agent and solubilizes the remaining acryl polymer revealing a fresh layer of paint. By this method, a more constant leaching rate and a continuous renewal of the substratum surface are achieved. To boost the antifouling activity of organotin, additional agents like cuprous oxide, cuprous thiocyanate, tributyltin fluoride may be mixed into the composition (De 1989b). This ingenious concoction provides almost complete antifouling protection for years, saves billions of dollars yearly, and helps "reduce the greenhouse effect" by reducing yearly fuel consumption by 7.2 million tons (International Maritime Organisation as cited in Collinson and Grant 1994).

Yet, there remains a drop of bitterness: TBT, most of the other heavy metal compounds, and some of their (bio-)degradation products are extremely toxic and extremely unspecific. The broad-spectrum activity of TBT against most prokaryotes and eukaryotes is based on its inhibition of ATP synthesis (Fukagawa and Suzuki 1993). Toxicity of TBT to diverse nontarget organisms has been found at exceptionally low levels (40 ng Sn/l for bivalves, 20 ng Sn/l for gastropods, 0.6 to 15 µg Sn/l for fishes; Batley et al. 1994). In the presence of other toxic compounds leaching from antifouling paints or other sources, toxicity levels of TBT may be expected to be much lower still, especially with regard to the observed synergism between TBT and copper uptake rates (Batley et al. 1994). In addition, TBT accumulates in the sediment and along food chains. Since the mid-1970s, environmental impacts of TBT contamination have been described (e.g., Claisse and Alzieu 1993). Nowadays, with the quasi-totality of large ships being protected by TBT-SPCs, things have everything but improved. In the 1980s several countries have half-heartedly banned TBT-based paints for boats under 25 m length (e.g., Canada, USA, Australia, Norway, Finland, most EU countries). This led to the return to copper-based antifouling paints and a subsequent rise of toxic Cu concentrations in some areas (Claisse and Alzieu 1993).

Real, environmentally harmless alternatives are very badly needed. Some of these, in variable states of development, will be presented in the following.

Change of medium

With the exception of some hardy intertidal aufwuchs organisms, most foulers are sensitive to exposure to air or freshwater. In Kiel (Germany), a fish farmer employs spherical net cages. These are suspended in rafts by horizontal axes at two opposing poles. Turned by 45 degrees once a week, each of the 8 net segments is exposed to air for 4 weeks, and immersed for the same period. Despite intense local fouling pressure in summer, these cages may be used for years without any further antifouling protection. On many coasts, small fishing crafts are hauled ashore after use or they fall dry at low tide. This exposure certainly slows down colonization by most foulers. Least affected will be emersion-adapted organisms like mussels and barnacles or borers sheltered within the wood.

As very few foulers are euhaline, periodical changes between saltwater and freshwater are likely to affect the fouling community severely. Many marinas and ports are built in the vicinity of estuaries. By channelling river water into the landside end of the port, one would create a brackish-water environment that might kill a good part of a ship's fouling community during its stay in the harbor. In the case of in-pipe fouling, an occasional backflushing with freshwater (if available) or hot sea-water (e.g., by reversal of the cooling system circulation) could represent a sufficiently severe disturbance of the fouling sequence.

Mechanical cleaning

A periodical disruption of the fouling sequence by mechanical brushing or scraping may suffice to keep fouling in an initial stage. This can be done by hand on the hulls of small boats, by divers, by brushes or glass shreds injected into pipes, or by underwater robots as developed for offshore drilling platforms (Pearce 1994). These robots could easily be adapted for cleaning ship hulls during harbor stay. If large vessels had their cleaning robot on board, which would do the fouling removal during unloading/loading in port, hull aufwuchs could be kept at an absolute minimum, especially since settlement is much reduced during cruising.

Electrochemical protection

Numerous attempts have been made to protect surfaces by electricity. Shibata et al. (1972) proposed the use of electrolyzed seawater as an antifouling mechanism. Of more common use is cathodic anticorrosion protection. A sacrificial anode or applied current leads to water hydrolization on the steel substratum and to an increase of pH (up to 11.5). This in turn provokes the precipitation of $CaCO_3$. This so-called scaling protects against corrosion, while the alkaline pH negatively affects biofilm formation and diatom settlement (Bhosle et al. 1993). Inversely, preformed biofilms may enhance or impair cathodic protection, depending on cathodic current density (Dexter and Lin 1991). On the other hand, there are no reports on cathodic currents significantly inhibiting settlement of macrofoulers.

Alternative coatings

Nonstick surfaces: It has already been mentioned that surface wettability affects adsorption and, even more so, attachment and adhesion of micro- and macrofoulers. In a range between 20 and 25 (or 30) mN/m, settlement and/or adhesion of macromolecules and bacteria (Dexter et al. 1975, Dexter 1976, Corpe 1982, Goupil et al. 1973, Busscher 1985), of diatoms and protozoa (Becker and Wahl 1991), of some macroalgae (Fletcher and Baier 1984, Becker and Wahl 1991), of mussels (Becker and Wahl 1991), and of barnacles (Griffith and Bultman 1980) are reported reduced for the species investigated. However, in Becker and Wahl's (1991) in-situ studies with natural mixed populations a second initial settlement minimum was frequently found at elevated surface tensions and, at least for diatoms and protozoa, a disappearance of all minima within two months. With time, certain foulers seem to be able to compensate for a lack of suitable bonding sites by enlarging their attachment pads (Fletcher and Baier 1984) and/or by modifying their glues (Becker 1994).

Nonstick antifouling paints or "fouling release coatings" are usually silicone rubbers, fluorinated epoxies or polyurethanes, or combinations of these (De 1989a, Wallis and Strudwick 1990). Initial problems of application and durability are slowly being overcome (Wallis and Strudwick 1990). Their performance is generally reported as "promising" but not yet "satisfying", the latter only when combined with biocides. The improvement of toxin-free nonstick paints should be encouraged. Yet, many of the compounds used for fouling release coatings are remarkably resistant to biodegradation. Their environmentally safe removal after service should be ensured before large scale use.

Ablative coatings: Compositions of different resins have been developed that erode from the painted surface in a controlled manner. This continuous renewal of the hull surface reportedly ensured satisfying fouling reduction for about three years (Foster 1994). The question is,

what happens to the potentially enormous amounts of resins released into the sea? Biodegradability and its breakdown products, accumulation phenomena, clogging of filtering organs or gills, etc. should be assessed before environmental problems arise.

Nonleach coatings: The concept of this type of protective paint is based on the permanent bonding of biocides to a water-insoluble matrix surface. Their toxic effect is limited to contacting organisms, does not affect nontarget organisms and the biocides would not accumulate in seawater, sediment or food chains. This is true to the principle of not putting into the sea what does not belong there, and thus constitutes a real improvement over current TBT-SPCs. Clarkson and Evans (1993) tested a silane-coupled quartenary ammonium compound against a fouling diatom. While the compound proved active, the coupling was insufficient, and rapid leaching occurred. Hopefully, the system can be improved by altering the coupling mode or changing the matrix.

Repellent surface structure: As mentioned above, small scale topography of a surface is likely to affect settlement through surface-near hydrodynamics and/or suitability of attachment area. Forsberg (1994) reports on the performance of substrata covered at various densities by vertically standing textile fibers. In these in-situ assays, the presence of fibers impeded mussel development and completely inhibited barnacle fouling. If other macrofoulers are affected similarly and over the generally required service life of five years, and if the fibers do not severely increase frictional drag, this concept might be a very promising alternative to current antifouling techniques.

Other approaches

Planting high densities of iron nails in stationary wooden structures impedes borer attack, probably caused by the toxicity of rust (Rao et al. 1991).

Replacing TBT or copper of standard antifouling paints by other biocides like chromated copper-arsenate (Weis et al. 1993) or antibiotics (Henschel and Cook 1990, Peterson et al. 1993) is a doubtful and maybe dangerous undertaking. Either these agents are specific and will, at best, inhibit a minor part of the colonizer pool, or their toxicity is general and, consequently, unspecific and will affect nontarget species.

In the last 30 years, the chemical industry has produced an amazing assortment of agricultural herbicides and pesticides. The frantic effort to replace heavy metals in antifouling paints has led to suggestions to employ these products as antifoulants. Yet, there is no indication whatsoever that these compounds, many of which are broad spectrum biocides and/or neurotoxins, would be less polluting than TBT or copper. The whole idea to substitute leaching broad-spectrum poisons by leaching broad-spectrum poisons is surprisingly unimaginative.

For the moment, it may be wiser to stick to the known dangers and damages caused by TBT-SPCs than to introduce on a large scale new, not surface-stationary antifouling compounds, the environmental impact of which might only be discovered years from now.

The perspective of natural antifoulants (biogenic biocides) will be treated in the last section of this contribution.

Epibiosis

Definition

Epibiosis is the association between sessile organisms growing attached to the body surface of living organisms. The basibiont constitutes the attachment substratum for the epibiont. No further interactions between the two partners are required by the definition, although they may occur (see below). In most cases, the association seems to be facultative: representatives of the basibiont species may be found bearing other epibionts or, with a clean surface, the epibiont species may be encountered on other basibiont species or on hard bottom. Species-specific associations of a symbiotic type are probably the exception in epibiosis. While epibiotic associations are encountered in all hard bottom communities, their distribution is not necessarily homogeneous.

Occurrence

General

Epibiotic associations are commonly encountered in the sea. Especially so, in those places where factors other than attachment sites are not limiting (nutritional conditions, predation, parasitism, salinity, temperature, etc.). Frequency of mechanical, physical, and biological disturbance and intensity of basibiont antifouling defense adversely affect epibiosis.

Geographical level

A decrease of fouling pressure with depth and latitude has been postulated (e.g., Richmond and Seed 1991). This may or may not apply to epibiosis as well. Biological parameters said to correlate with these gradients (individual longevity, generation time, species numbers, diversity, secondary metabolite production, etc.) are proper to both epibionts

and basibionts. Thus, the relationships between epibionts and basibionts might not change drastically when going north or down. The fact that numerous species may be both, epi- or basibiont, alternatively or simultaneously, certainly contributes to such a presumed levelling out of geographical effects. The impression (personal observation) is that the degree of epibiosis varies more with water quality than with latitude: often, epibiosis seems especially intense in ports or near waste-water outflows. Probably, either basibionts are weakened by bad water quality and/or epibiont growth is boosted by high nutrient levels in these localities. Regrettably, no literature is available on this subject.

Species level

Epibiosis varies enormously among species. This applies both to quantity and quality of epibiosis, or susceptibility to and specificity of epibiosis.

Susceptibility: Tolerance of epibiosis seems to depend on the biological role of a potential basibiont's body surface. Numerous species rely on a clean 'skin' for various functions: photosynthesis (plants, or animals with photosynthetic symbionts), gaseous exchange, nutrient uptake and excretion (algae, many thin-skinned invertebrates), filtration (sponges, colonial ascidians), trapping of food particles (enteropneusts, many polychaetes, many cnidaria, bryozoa), low-friction swimming (many fishes and aquatic mammals, squids, numerous plankton organisms) just to name some examples.

On the other hand, many species secrete thick cuticles or shells whose biological functions are less impeded by the presence of epibionts: prosobranch gastropods, bivalves, tube-building polychaetes, crustaceans, solitary ascidians, etc. As epibiosis may have disadvantages other than insulation of biologically active surfaces (see below), not all sessile shelled animals carry epibionts. But as a rule, in a given habitat, algae are cleaner than seagrass (nutrient uptake by roots in the latter case), colonial ascidians with tiny filtration pores all over their surface are cleaner than solitary ones, cephalopods are cleaner than shelled molluscs, highly motile pelagic fishes are cleaner than some sluggish benthic fishes (e.g., stone fish), and so on.

Specificity: There are amazingly few reports on species-specific epibiotic associations, but this may be due to the scarcity of investigations in this domain. The problem with many reports on epibioses is that they often are more qualitative than quantitative circumstantial observations. Thus, *a posteriori*, it is difficult to retrace whether a given epibiont species occurs sporadically or regularly, in high or low abundance, seasonally or

year-round, locally or on all populations of the basibiont species, on one or many substratum species, and on hard substrata as well.

From the epibiont point of view, substratum specificity can express itself at different levels. Facultative epibionts are found indiscriminately on basibionts and hard substrata. Strict epibionts settle exclusively on living organisms, but may or may not exhibit preferences for certain taxa or species of basibionts. While there are examples for some basibiont specificity in epibionts [(e.g., certain bacterial strains on tuna and barracuda (Sar and Rosenberg 1987), bacteria on crustacean embryos (Gil-Turnes et al. 1989), bacteria on coralline algae (Johnson et al. 1991), protozoans on pelagic crustaceans (Chiavelli et al. 1993), the well known cases of *Hydractinia echinata* and *Adamsia palliata* on hermit crabs, *Polysiphonia lanosa* mostly on *Ascophyllum nodosum* (Lining and Garbary 1992), kamptozoa only on living substrata (Cori 1936, Dyrynda 1985)], most organisms found growing in living substrata are facultative epibionts belonging to the local aufwuchs community (e.g., Harlin 1980, Cattaneo 1983, D'Antonio 1985, Horner 1987, Otero-Schmitt and Sanjuan 1992, Gaiser and Bachmann 1993).

Interestingly, there are few reports on intraspecific epibiosis, e.g., conspecifics growing on one another. Examples are gregarious animals like balanids, mussels, the polychaetes *Hydroides, Pharagmatopoma* or *Filgrana,* and others. But the majority of facultative epibionts, and especially algae, have not been observed on conspecifics. Either intraspecific epibiosis is exceptional (for unknown reasons), or conspecific epibionts were not recognized as such, but taken for parts of the basibiont. It could be rewarding to look into this problem.

Individual level: Within potential basibiont species, individuals differ by their susceptibility to colonization. Especially in species reported usually clean, one may occasionally find representatives that do bear epibionts. Probably, this reflects a suspension of antifouling defense in individuals of old age, in stressful habitats, during inactivity phases, etc. For example, crustaceans may become colonized when molting intervals increase due to low temperatures, rhizocephalan parasitism, old age, gestation (e.g., Abello and Macpherson 1992, Allen et al. 1993), when grooming appendages are lost (Bauer 1989) or when unable to burrow (Becker and Wahl, 1996) littorinid gastropods may become subject to epibiosis when shell grazing by conspecifics decreases (Wahl and Sönnichsen 1992), a didemnid ascidian *Polysyncraton lacazei* exhibits intensified epibiosis when sporadically going through a phase of inner rejuvenation, during which the colony surface is sealed by a cuticle (Wahl and Lafargue 1990), and so on. These few examples, once again, illustrate the omnipresence of colonization pressure: epibionts settle as soon as defense or disturbance lessen in intensity.

Organ level: Even on epibiotized individuals, epibionts are not distributed homogeneously. Two distributional patterns have been observed. Qualitatively, different colonizer species frequently select different parts of the basibiont directed either by physicochemical properties or hydrodynamic conditions in different regions on the substratum organism (e.g., Baker and Orr 1986, Durante and Chia 1991, Otero-Schmitt and Sanjuan 1992, Rajaguru and Shanta 1992, Martinez and Correa 1993, Bergey and Resh 1994, Gaiser and Bachmann 1994). This settlement selectivity may be passive (avoiding regions of high defense level) or active (cueing on codes proper to favorable positions). Illustrating the second, *Balanus improvisus* settles preferentially in the trophically advantageous near-siphon region of mussels (Laihonen and Furmann 1986), bacteria attach near the nutrient-releasing slits and pores of the diatom *Navicula confervacea* (Rosowski 1992), bryozoan larvae selectively settle on the youngest blade portions (with highest life expectancy, Durante and Chia 1991). Numerous further examples can be found in the literature. Differential mortality, too, may result in heterogeneous distribution of epibionts (Keough 1986).

Quantitatively, density of epibiosis may be conspicuously reduced on certain organs. This is probably due to an uneven distribution of defenses (see below) across the basibiont's body surface. Even on notoriously epibiotized species, body openings, sense organs, joints, and reproductive organs, or photosynthetically important tissues are generally free of epibiosis. This is not really surprising, since evolutionarily it would be a short-lived strategy to leave these vital parts undefended. A most impressive example is the solitary ascidian *Microcosmus sabatieri*, which is covered by an extremely diverse epibiotic community except for its shockingly clean siphon openings.

Season level: In temperate zones, species composition and conspicuousness of epibiosis often follows a yearly cycle (e.g., Mazure and Field 1980, Sieburth and Tootle 1981, Thelin and Bedhomme 1983). Water quality (temperature, nutrient levels, etc.), relative abundance, and metabolism of basi- and epibionts vary with season. High colonizer abundance, low basibiont activity (and defense!), and high nutrient concentrations (possibly making attachment site the limiting factor) should favor epibiosis. In the Baltic Sea, this constellation seems to occur in (late) summer, when many macroalgae have reached the end of their growing season and become densely overgrown by filamentous algae (*Polysyphonia* sp., *Ectocarpus* sp.), hydrozoans, mussels, and other epibionts (personal observation).

Table 2. Potential beneficial and detrimental effects of epibiosis on epibionts and basibionts.

Beneficial Effects	Detrimental Effects
Epibionts	
Gain of attachment site	Unstable substratum
Expanding substratum	Exuded toxin stress
Exuded nutrients from basibionts	Risky habitat changes
Favorable hydrodynamics	Shared doom
Shock-absorbing substratum	
Favorable irradiation	
Free transportation	
Associational resistance	
Basibionts	
Camouflage	Weight increase
Protection	Drag and friction increase
Nutrients or vitamins from epibionts	Flexibility decrease
Drag reduction	Brittleness increase
Improvement of housing	Siltation increase
Associational resistance	Insulation effect
	Mechanical damage
	Chemical damage
	Competition for nutrients
	Shared doom
	Increased susceptibility to predation

Effects of Epibiosis

The question now arises about the ecological significance of epibiosis. What type of association is it? Should it be classified as mutualism, inquilinism, space-parasitism, phoresis...? Is it beneficial or detrimental from the basibiont's or the epibiont's point of view? Or can it be both, simultaneously or sequentially or depending on season, habitat, predators, etc.? Table 2 gives a very schematic overview of the potential effects of epibiosis on one or the other partner.

Previously, the effects of epibiosis and defense mechanisms have both been reviewed in detail (Wahl 1989 with relevant literature), thus, the following two sections will be treated rather briefly. Some new findings (and the corresponding references) are given here.

Benefits for epibionts

Gain of attachment site: Obviously, the biggest advantage of settling on (living) substratum is to have found available free space for attachment, which, in many cases, is a prerequisite for further development. Nearby hard bottom may be hopelessly overcrowded, yet living substratum in

contrast to hard bottom is continuously formed anew. A rocky wall, once completely encrusted will probably stay so, at least until the next major disturbance. Available space on living surface, on the other hand, is always created by settlement and growth of (potential) basibionts.

Expanding substratum: A further advantage of settling on living substrata, especially near meristems, is that in the immediate vicinity of the epibiont new colonizable area appears by growth. If the new epibiont is endowed with the capacity for asexual reproduction and/or lateral colonial growth, this successful genotype may fast be multiplied.

Exuded nutrients: Most organisms leak, leaching (among other compounts) amino acids, peptides, sugars and lipids that may serve as nutrients to others. Bacteria are known to thrive on these exudates, but it seems plausible to presume that many others do, too, at least as an accessory nutrient source. Exudate concentration diminishes exponentially with distance from the leaking surface. In this regard, epibiosis offers an ideal position. Bacteria and phototrophic epibionts may benefit from nutrients contained in host excreta (Threlkeld et al. 1993, Bergey and Resh 1994).

Favorable hydrodynamics: Current velocities and water exchange are slow on the rock wall deep within a dense, bushy aufwuchs community. The closer to the rock face you live, the calmer it becomes. ('no-slip' condition). Small and/or flat organisms (bacteria, microalgae, 'two-dimensional' growth forms like some encrusting algae, porifera, colonial ascidians, bryzoans, etc.) might under such conditions have problems attaining oxygen and suspended food particles or evacuating their waste products (e.g., Kaspar 1992). Living on gorgonian branches or the distal parts of macroalgae, could be hydrodynamically rewarding.

Shock-absorbing substratum: The really tempting thing about living hydrodynamically exposed on a kelp or a seagrass blade, is that the advantage of good water exchange is largely decoupled from the risk of extreme water velocities: the flexibility of the substratum permits a passive retreat of host and epibiont into calmer strata nearer to the hard bottom.

Favorable irradiation: When light is limiting, an exposed epibiotic position offers better conditions than the shady understory.

Free transportation: With regard to water exchange around an epibiont it is irrelevant whether the ocean flows past the substratum (e.g., epibiont on benthic aufwuchs) or the substratum moves through the ocean

(epibionts on cetaceans, sea turtles, etc.). Access to dissolved nutrients may be facilitated by a thinner diffusion boundary layer on the surface of swimming hosts (Threlkeld et al. 1993).

Associational resistance: If a basibiont is well defended against predation, an associated epibiont might benefit from this protective shield, especially if the epibiont blends in well with the host background (color, shape, smell; see defense section). A special case of escape from predation is the settlement of epibionts on the body surface of their potential predator, thus obtaining an out-of-reach position (Threlkeld and Willey 1993).

Disadvantages for epibionts

Unstable substratum: The main inconvenience of epibiotic life is the unstable nature of the living substratum. This unstability has chemical, structural, and temporal aspects.

Chemically, the molecular composition of the basibiont's surface, as well as the nature of its exudates are likely to vary with the physiology of the host, which itself will be controlled by age, season, water quality, stress, disturbance, epibiosis, etc.

Structurally, living surfaces often bend and twist, expand or branch during growth, develop three-dimensional topography.

Temporally, a living surface may be renewed by loss of scales, mucous production, sloughing. At a quite unpredictable moment the surface may vanish through predation, disturbance or natural death of the basibiont.

Epibiont traits allowing to cope with this complex unstability would be: settlement selection of more reliable basibionts, or short generation time plus small size/small attachment area/flexibility plus low sensitivity towards harmful exudates.

Exuded toxins: Some of the exudates may exhibit antifouling activity (see defense section). Epibionts settling on defended substrata, obviously should be resistant to the defense(s). Adapted epibionts may cue on these toxins, thus escaping competition and predation.

Risky habitat changes: Epibionts 'boarding' motile basibionts run the risk of encountering environmental conditions beyond their range of tolerance: e.g., algae settling on crabs that migrate below the euphotic zone or hide in the shade during daylight hours; marine epibionts on turtles will (during nesting of the host) be exposed to sand abrasion, air, sun, and maybe rain; epibionts on whales will encounter (during the yearly migration cycle) extreme ranges of salinity and temperature; on a smaller

scale, even on sluggishly moving basibionts, the settlers may be carried into the shade, onto land, into hydrodynamically unfavorable conditions, into contact with harmful organisms and so on.

Shared doom: By definition, the epibiont lives at the interface between basibiont and ocean, which is whence most danger comes. Many predators of the substratum species will not be deterred by the presence of epibiosis, and consume the entire association.

Benefits for basibionts

Camouflage: A dense epibiotic cover may shield the host from detection by predators. Optically searching predators may be confused by a change of contour, shape, and color. Other predators cue on prey exudates. If these are used up by epibionts or masked by epibiont exudates, the substratum organisms may become untraceable.

Protection: The insulating effects of epibiosis, already mentioned in the context of transcutaneous exchanges, in certain circumstances may be beneficial. Medium change during emersion at low tide represents severe stress for intertidal animals and plants. The effects of irradiation (in particular elevated UV levels), heating, desiccation, desalination by rain and freezing on intertidal organisms may be substantially dampened by epibionts (e.g., Dayton 1971, Penhale 1977). It is also conceivable that mechanical shocks (driftwood, ice, hail, sand grains in high velocity habitats) are absorbed by certain epibionts.

Nutrients or vitamins from the epibiont: Like the basibionts, many epibionts species produce and exude organic substances that may be taken up by the host. Thus, in the epibiotic layer and near the basibiont surface, conditions could be favorably enriched in peptides, sugars, lipids, CO_2 and N_2 (usable by algal hosts, e.g., Goering and Parker 1972), vitamins from bacteria (e.g., Lynch et al. 1979) and so on. Especially, in waters deficient in one or more of these essential compounds, certain epibionts (bacteria and microalgae, in particular) could provide missing items. In some cases, epibionts may be directly consumed by their hosts. Possibly, some corals feed on bacteria cultured in excreted surface mucus (Paul et al. 1986). Caddis flies graze microalgae on the front part of their cases (Bergey and Resh 1994). Some nematodes "culture" specific strains of bacteria on their cuticle, "walk" them through nutrient-rich sediment, and feed on them (Polz et al. 1992). Many more examples exist.

Drag reduction: As will be treated later on, aufwuchs generally increases surface friction and drag. There seem to be exceptions to this rule. Sar and Rosenberg (1987) describe the epibiotic association between certain hydrophobic bacteria and fast swimming fishes. In these cases, the microbes have a beneficial effect by reducing drag on the fish skin. Other examples are imaginable: why shouldn't filamentous algae reduce turbulence (and consequently drag) around a hydrodynamically poor shape (gastropod or bivalve shell)? Smooth, soft epibiotic crusts like didemnids or sponges covering rough basibiont surfaces could have similar effects. There appear to be no investigations in this direction.

Housing improvement: Hermit crabs often occupy empty gastropod shells. These not always suit the occupant perfectly in size or shape. Certain epibiotic bryozoans grow beyond the rim of the last convolution, thus enlarging shelter space and reducing the frequency of hazardous shell change by the crab (Taylor et al. 1989). In another case, an unbalance of hermit crab shells can be corrected by the crab selectively placing epibiotic anemones on shell areas that are too light (Brooks 1989).

Associational resistance: Certain epibionts may offer antipredator or antiepibiosis defense to their host. Optical or chemical cues of the host may be masked by the epibionts so that the substratum species is not recognized by potential colonizers or predators. Defenses or the consistency of the epibionts may make handling by predators difficult. Some examples for associational resistance will be given under "Synecological effects" and "Defense".

Disadvantages for basibionts

At first glance, the detrimental effects of epibiosis on basibionts seem to outweigh the benefits, at least by number.

Weight increase: Many epibionts, in particular those producing calcareous tissues or structures, are denser than seawater. Their settlement and growth increase the weight of the living substratum. This decreases the buoyancy on which many pelagic species (fishes, turtles, seagrasses, algae, etc.) depend. Compensation by increased swimming activity or additional air bladders, fat or oil droplets is likely to be energy consuming (e.g., Allen et al. 1994), but additional physiological costs caused by epibionts may be tolerable in nutrient-rich habitats (Threlkeld et al. 1993). If the loss of buoyancy is not (sufficiently) compensated, the basibiont will sink and possibly meet intolerable conditions with regard to light, water flow, oxygen tension, and the like. On the Swedish coast, there are whole kelp beds lying flat and rotting under the influence of

weight-increasing epibiotic bryozoans, polychaetes and algae (personal observation). In the Baltic sea, extreme spatfalls of mussels may flatten seagrass beds. Pelagic crustaceans have been reported to sink faster under the load of epibiotic diatoms (Allen et al. 1994). In contrast, Threlkeld et al. (1993) report that accelerated sinking was restricted to dead or preserved specimens, while living copepods sank slower, presumably due to drag increase.

Drag and friction increase: Generally, micro- and macroaufwuchs increase frictional drag on surfaces (see also section on fouling). So do most epibionts (e.g., Dixon et al. 1981). According to unpublished data (publication in preparation), balanid and filamentous algal epibionts increase drag on *Littorina littorea* by 40 to 250%. Interestingly, this species is significantly less fouled in high turbulence North Sea intertidal areas than in calm Baltic subtidal habitats. This is due to differences in population density differences that lead to reduced mutual grazing between conspecies in the sparser Baltic population (Wahl and Sönnichsen 1992). An additional reason may be that snails with epibionts survive less well in exposed habitats. Mussels with kelp epibionts are reported to be dislodged more easily than clean conspecifics (Witman and Suchanek 1984).

Changes of flexibility and brittleness: In wave-swept habitats, algae and other sessile, upright aufwuchs organisms depend on flexibility and toughness for survival (e.g., Denny 1988, Gaylord et al. 1994). Given the physical properties of the medium (high density, high viscosity), rigid resistance to strong water velocities is acceptable only in close proximity to the substratum, and thus restricted to low growth forms like barnacles, limpets, and encrusting calcareous algae. Anything extending more than a few decimeters from the substratum must be yielding. Underwater trees are an impossible concept (e.g., Vogal 1981); they would be uprooted by the first moderate wave. Thus, any impairing of flexibility by calcareous, encrusting epibionts (bryozoans, corallinaceae, serpulid polychaetes, etc.) could be detrimental, increasing brittleness and risk of breakage.

Siltation increase: Any aufwuchs community composed of upright, possibly branching forms will slow down water velocities across the substratum and create calm zones within the community. More and finer sediment will settle in these zones, less will be resuspended. This increased siltation may lead to anoxic conditions on a basibionts surface and contribute to the insulating effect.

Insulation effect: Insulation by an epibiotic community comprises two aspects: shading and suffocation/starvation. Dense, nontransparent

epibiotic coverage reduce irradiation of the basibiont surface substantially. If, as a consequence, photosynthesis decreases below the compensation point, the seagrasses or algae will die. Decay of whole seagrass meadows have been attributed to shading by epibionts (Sand-Jensen 1977, Bulthuis and Woelkerling 1983). On the other hand, water exchange near the basibionts surface may be severely reduced by epibiosis. Supply of gases and nutrients as well as evacuation of wastes will be slowed down.

Mechanical damage: Borers and the attachment organs of epibionts ('roots', crampons, kenozooids, suction cups, rigid cements, etc.) may injure the basibiont surface by penetration or by a stressful difference in flexibility/rigidity between substratum and settler.

Chemical damage: In the fouling section it is mentioned how, within biofilm and below macrofoulers, physicochemical conditions can be quite aggressive. Bacterial enzymes, oxygen deficiency, highly alkaline or extremely acid pH, accumulation of toxic wastes etc. are likely to chemically attack many basibionts' surfaces.

Competition for nutrients: If epibionts and substratum organisms have the same trophic requirements, they may experience competition for nutrients. This could be the case for algae on algae, filter feeders on filter feeders, and so on. As the epibionts are usually positioned upstream, such a niche overlap would mainly inconvenience the basibiont. However, if the basibiont's filtering capacity clearly exceeds those of its epibionts, their presence does not necessarily affect the former (Laihonen and Furmann 1986, Lesser et al. 1992).

Shared doom: Epibiont predators or grazers often increase basibiont survival or productivity by limiting the negative effects of epibiosis (e.g., Brönmark 1985, Howard and Short 1986). But in biting, picking or shaving off of epibionts they frequently injure basibiont tissue. The damage may go a lot further. We have recently studied the influence of epibionts on different host algae's susceptibility towards urchin grazing (Wahl and Hay 1995). In a clean state, some of the basibiont algae, e.g., *Sargassum filipendula, Zonaria tournefortii* or *Codium fragile*, were of low preference and probably not consumed in the field by the urchins (*Arbacia punctulata*). However, when overgrown by high preference epibionts like bryozoans, gastropod eggs or certain red algae, the urchins often continued feeding on the host after having consumed the epibionts. This fateful aspect of an epibiotic association is coined 'shared doom'. Likewise we recently found (Molis and Wahl, in preparation), that the

presence of epibiotic balanids significantly and substantially increased a mussel's susceptibility towards predation by the shore crab *Carcinus maenas* compared to clean mussel individuals.

Increased susceptibility to predation: It is conceivable that the presence of epibionts neutralizes host adaptations against predation by effects other than shared doom. Negative cues or defensive compounds on the host surface could be masked or metabolized. Escape strategies like small size or transparency, in particular of planktonic basibionts, may be counteracted by conspicuous (large or colored) epibionts. Thus, epibionts on zooplankton have been suggested to increase their susceptibility to salamander or fish predation by adding color/contrast, by increasing optical conspicuousness or slowing down escape movements (Threlkeld et al. 1993, Threlkeld and Willey 1993).

Synecological effects

In the previous section, some of the more important effects of epibiosis on either partner of the association have been presented. The consequences of epibiosis in any given association will depend on the actual combination of the above factors acting (which is a function of epibiont biology and morphology plus physical habitat characteristics) and on the basibiont species' susceptibility to these factors or factor combinations.

Epibiosis may affect entire communities. For instance, when grazing pressure by herbivorous fishes or generalist urchins is intense, some palatable algae may survive only when growing epibiotically (and unconspicuously) on unpalatable host algae (Hay 1986). On the other hand, palatable algae can avoid predation when optically and chemically protected by unpalatable epibionts, as suggested in Wahl and Hay (1995). Thus, grazing pressure in combination with epibiosis effects may lead to a redistribution and selective survival of species within a community.

Eutrophication, the overabundance of nutrients, may (in the absence of grazer control, and under favorable light and temperature conditions) make attachment area the limiting factor for algal development. Living substrata will then be subject to intense colonization pressure. In the Baltic Sea, these conditions prevail from April through October. A subjective impression is, that in this region algal epibiosis on macroalgae is at its height in August and September. In spring and early summer, most macroalgae in this area show maximum activity and possibly highest defense levels (e.g., Sieburth and Tootle 1981). Dense epibiotic load may suffocate the host algae or provoke increased losses during the autumn storms. This must not necessarily be detrimental: as older plant parts generally have lower defense levels, they bear more

epibionts and will be the first to go during a storm. The removal of unproductive plant material will make room for new growth, reduce shading, and supply deeper shelf areas or beaches with organic material.

As shown for algal basibionts, many animal substrata only persist in a given habitat because they are protected by epibionts against certain predators. Bryozoans protect whelks against lobsters (Barkai and McQuaid 1988) and kelp against snail grazing (Durante and Chia 1991), hydrozoans protect mussels against shore crabs (Molis and Wahl, in preparation), sponges protect bivalves against starfish predation (Bloom 1975, Feifarek 1987).

For defense, some animals actively select protective epibionts and attach them onto their body surface. Certain pelagic amphipods grasp chemically defended pteropods to ward off predatory fishes (McClintock and Janssen 1990). The presence of predatory octopus may stimulate hermit crabs to attach more and strategically better placed anemones onto their shells (Brooks 1989).

Knowing that the disappearance of any of these epibiotically protected species, might lead to unpredictable changes in the community concerned, one may appreciate the ecological potentiality of epibiotic interactions.

Basibiont Reactions to Epibiosis

Hopefully, the previous section has convincingly shown that epibiosis cannot be classified as good or bad. The categories "space parasitism," "mutalism," etc. are too rigid to describe these complex associations. The relative importance of beneficial and detrimental effects depends on who is colonized by whom, in the presence of who else, and when and where. Thus, increase of surface friction is no problem in stagnant water, weight increase is irrelevant for encrusting basibionts, shared doom effects only catch in the presence of a predator, insulation effects only when the concerned surface area is engaged in transcutaneous exchanges, etc. One of the most luxuriantly epibiotized organisms known is the solitary ascidian *Microcosmus sabatieri*. It has been reported to regularly bear more than 70 species of animal macroepibionts in its tunica (Monniot 1961)—macroalgae, diatoms, protozoa and bacteria not counted. The density of the epibiotic community is such that discovering the pear-sized animal on a rock wall is difficult, and often only possible when the perfectly clean and conspicuously colored siphons are everted. Obviously, this species does not suffer from epibiosis. It is an animal (no shading effects), living attached (no weight effects) in calm water zones (minimal drag effects), covered by a tough outer tunica (no insulation

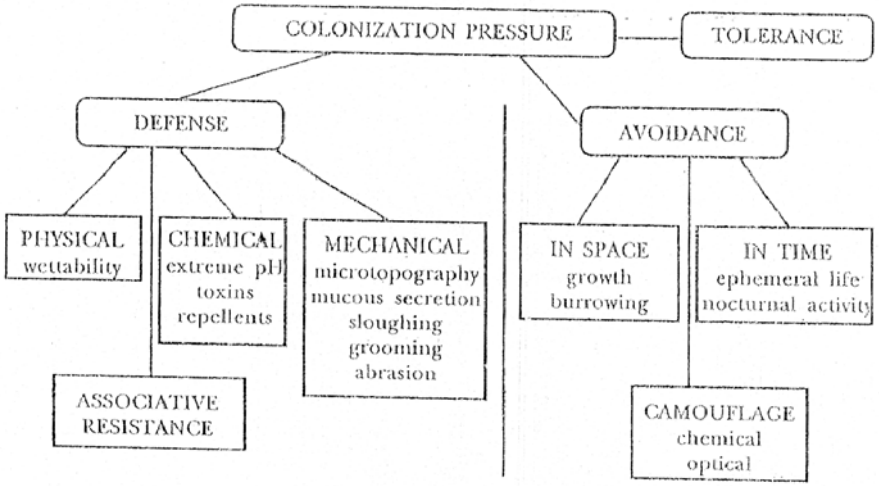

Figure 3. Possible adaptations of potential basibionts in face of colonization pressure.

effects, mechanical or chemical damage), and is a powerful filter feeder (no trophic competiton).

Naturally, there are numerous species less tolerant to epibiosis. When some basic biological activity would be impaired by epibiosis, like swimming in fishes for instance, the nontolerance is permanent. But often epibiosis is only harmful during certain life phases or on certain organs. A partial (spatial or temporal) tolerance to colonization is common: older leaves of seagrasses, stipes or holdfasts of many algae, chitinous or calcareous shells and tubes of animals, whole animals towards the end of molting or sloughing intervals (crustaceans, algae, sponges, ascidians), or during phases of inactivity (e.g., didemnid *Polysyncraton lacazei*). As already mentioned, body areas nearly always kept clean are sense organs, body orifices, reproductive organs, filters, joints, gills, some photosynthetic tissue.

With regard to epibiosis, one may observe three major strategies in marine organisms: avoidance, tolerance (as mentioned above) or defense. Naturally, intermediate position and combinations of different strategies are common, maybe even the rule, figure 3.

Avoidance

This term is admittedly used in a very broad sense here, including behavioral and life history aspects that allow a potential basibiont to elude colonization.

In time: Extremely short-lived organisms (bacteria, some unicellulars) will simply not be exposed to colonization long enough, at least for the slower aufwuchs steps to establish. Additionally, these ephemeral life forms are usually too small to represent a suitable colonization substratum. A partial retreat from colonization is ensured by sciaphilic behavior: nocturnal activity and diurnal retreat into shade should substantially reduce colonization by photosynthetic epibionts (Becker and Wahl, submitted). Analogously, in temperate areas, winter activity and summer diapause would help avoid periods of maximal colonization pressure. There are no known observations in this regard. But several macroalgae are known to have their peak of activity in winter or early spring, well ahead of meroplanktonic blooms. This may have other evolutionary causes (e.g., high nutrient concentration, inactivity of herbivores in winter/spring), but epibiosis would certainly be a negligible problem for these organisms compared to summer algae.

In space: Colonization takes time (see above). Growth may be fast enough to outrun epibiosis, and always dispose of sufficiently large areas of clean, e.g., photosynthetically active, tissue to survive. The near-meristematic parts of most algae and seagrasses are usually clean. This is not always due to fast growth alone. Frequently, levels of defensive secondary metabolites are elevated in these youngest plant parts. By leaching and gradually declining production rates, their concentration declines with tissue age. Nevertheless, growth rates of several cm to several dm per day (seagrasses and giant kelp, respectively), do represent a pace that colonization cannot keep up with.

Epibiosis can be avoided by living in habitats not exposed to colonization. A boring or burrowing mode of life in a hard or soft bottom would drastically reduce the number of settlers. In addition, the constant abrasion and friction between sediment and body surface should remove most multicellular epibionts. Diatoms would perish for lack of light. Indeed, the only epibionts frequently found on burrowing organisms are bacteria.

Camouflage: As mentioned before, settlement of many sessile species is directed by positive and negative cues. A normally suitable substratum organism could suppress positive cues, secrete negative cues or tolerate epibionts that do this. The tunicate *Ciona intestinalis* bears a strongly fouling inhibiting bacterial strain on its surface (Kjelleberg and Holmstroem 1994).

Defense

Physical: As we have seen in the fouling section, substratum wettability is supposed to strongly influence macromolecule adsorption, bacterial

adsorption as well as the adhesion of all colonizing organisms. While there is evidence for the validity of this effect in the initial stages of colonization, attached life seems to be more adaptable than previously thought. By increasing the area of attachment or by changing the chemistry of their glues or cements, colonizers are capable of compensating for the initially unfavorable surface conditions (e.g., Fletcher and Baier 1984). For instance, the adhesion strength of bacteria on fouling release surfaces (20–30 mN/m) within days or weeks approaches that on most other substrata (Becker 1994). Could that be the reason why this antiepibiosis defense seems to be so rare at least in larger organisms? At first glance, this strategy appears tempting, indeed: surface-stationary, nontoxic, permanent, metabolically cheap, broad-spectrum. However, reduced adhesion would only impede aufwuchs in the presence of shear stress, i.e., in turbulent or high velocity habitats or on fast moving animals. Therefore, this defense would be useless to all drifting organisms and to all those living in calm habitats or protected strata of the aufwuchs community. The only marine organisms with surface wettabilities near the critical 20–30 mN/m range are certain bacteria (e.g., Fattom and Shilo 1984), several species of copepods (personal observation), and possibly Sar and Rosenberg's (1987) fishes bearing hydrophobic bacteria on their skins. Vrolijk et al. (1990) measured hydrophobic wettability (24-27 mN/m) values on gorgonian surfaces. But, this report should be viewed with some caution because the results were obtained on previously air-dried tissue (surface cracking?) and by organic solvents (dissolution of surface compounds?). Using living specimens and nonaggressive methods (air-bubble contact angle, e.g., Wahl and Banaigs 1990), only one hydrophobic species, *Alphaeus* sp., in a screening of about 100 marine Mediterranean, Baltic, Pacific, and Indo-Pacific ascidian and decapod crustacean species (Becker 1994; Becker and Wahl, submitted and personal observation) was found. Linskens (1963) and Ballentine (1979) suggested the existence of hydrophobic surfaces in macroalgae, but no subsequent study has taken up these ideas. For the time being, unfortunately, unwettable biological surfaces have to remain an extremely interesting, albeit hypothetical, antiepibiosis strategy.

Chemical

• pH: Numerous organisms are known to create nonneutral pH conditions at their surfaces. Acid surfaces have been found in certain species of gastropods (Marbach and Tsurnamal 1973, Mebs 1985), ophiurids (Fontaine 1964), and tunicates (Davis and Wright 1989, personal observation). Baker and Orr (1986) describe highly alkaline leaf surfaces in aquatic plants and suggest that this may be an antiepibiosis adaptation. Likewise, Stoecker (1978) postulated that acid surface conditions in ascidians contributed to epibiont reduction. Her methods and conclusions, however, were questioned by Parry (1984) and Davis and Wright (1989). The latter concluded that acidity was no effective antifouling defense in the sea. It should, indeed, be quite energy consuming to uphold an extreme pH value against the high buffering capacity of seawater. Baker and Orr's (1984) work was done in freshwater, which is a less good buffer. Additionally, the high pH in this case was a by-product of normal metabolism and thus not costly.

• Toxins: In the last 15 years, chemists have isolated an impressive number of secondary metabolites from marine organisms: bacteria, cyanobacteria, algae, and animals. Fortunately, John Faulkner tries to keep up with the rapid pace of extraction, purification, identification, and description in his yearly *Marine Natural Products* series (appearing in *Natural Products Reports*). Secondary metabolites are hard to define. This notion comprises all organic compounds that initially researchers do not know what the extracted organism used them for. They may be by products or intermediary products of the primary metabolism, they may be storage products or wastes, but they may also have an ecological function, like messenger molecules or pheromones, antipredator or antiparasite defense, etc. Because for most investigators it is unsatisfactory to find something without knowing what it is, many first descriptions of marine natural products are accompanied by a lot of speculation about the substance's possible function in life. This may be confusing when the speculation is not clearly marked as such. Extrapolations from Petri dish to marine benthos communities should be made with great caution. Not every substance found active against a human pathogen in vitro impedes bacterial epibiosis in vivo. Not every antimitotic compound will inhibit metamorphosis of larvae settling on the organism considered.

To test the hypothesis that a species exhibits chemical antiepibiosis defenses: (1) only the body surface of an organism (i.e., the defensive interface) should be extracted, (2) compounds or naturally proportioned mixtures of compounds should be tested in (sub-) natural concentrations, (3) embedded in a nontoxic matrix, (4) exposed in the extracted organism's habitat for a (5) sufficiently long time. Only very few studies meet these five criteria. To screen generally for antifouling activities, regardless of the compound's natural in-vivo role and probably with an ulterior technical application in mind, only criteria 3 and 5 are of relevance. But in this case, an environmental toxicity evaluation of promising compounds should be an absolute prerequisite for recommendation.

Natural antiepibiosis (antifouling) chemical activities have been suggested for numerous marine organisms (reviewed by Bakus et al. 1986, Davis et al. 1989, Paul 1992, and the Faulkner series). Here are some examples from recent literature: Benthic bacteria chemically inhibit settlement of ascidian larvae (Kjelleberg and Holmstroem 1994). Algae produce antilarval and antibacterial compounds (Schmitt 1991, Steinberg 1994). Fatty acids from sponges (Goto et al. 1993) and from octocorals (Mizobuchi et al. 1993) impair mussel attachment, interestingly with activity directly correlating to number of double bonds for chain lengths between C10 and C20. Nonpolar sponge and bryozoan extracts, in contrast to aqueous extracts, to a large percentage inhibit settlement of ascidian and bryozoan larvae (Altena and Butler 1994). Polar and nonpolar extracts from gorgonians may exhibit antidiatom activity (Targett 1988). Terpenoid compounds of octocorals are reported to reduce algal growth (Coll et al. 1987). Extracts from ascidians show antibacterial, antidiatom, antifungal, and antilarval activity (Davis and Wright 1989, Wahl and Banaigs 1991). With the exception of some antilarval bioassays, in-vitro tests usually assess only growth and/or survival of the target organism. Consequently, most tests will only discover toxicity. Soft chemical antiepibiosis adaptations like absence of positive settlement cues, presence of negative cues or nontoxic repellence will go undetected.

• Repellence: Many settler species discriminate between diverse available substrata. Rejected surfaces may be simply unattractive (lack of positive cues) or actively repellent (production of compounds negatively influencing settlement behavior). Repellent compounds need not affect growth or survival of target organisms. Due to the inadequacy of most screening bioassays in this regard, the ecological importance of colonizer repellents may have been underestimated in the past. Cases of nontoxic repellent activity of natural compounds towards larval settlement have been reported (e.g., Maki et al. 1988). In a recent study, we have investigated the susceptibility of colonial ascidians to bacterial colonization (Wahl et al. 1994). Some of the results may be interesting in this context. Epibacterial density was drastically different on different ascidian species. Antibacterial activity (cytostatic/cytotoxic) did not correlate with epibacterial density. In contrast, bacteria-repellent, nontoxic activity did. The latter was assessed by incorporation of surface extracts at natural concentration in nontoxic agar, and exposition to colonization by bacterial strains isolated from ascidian surfaces. When comparing single conspecific colonies, nontoxic repellent activity was always present, toxic antibacterial activity was not. A note with regard to the extrapolation of in-vivo functions from in-vitro results: variability of antibacterial activity was high among ascidian colonies. Tested individually against 40 bacterial strains, only 42% of the interactions showed activity, some

colonies were completely inactive, other inhabited 80% of the strains. Pooled extraction of all colonies would have yielded a completely blurred result, indicating a moderately strong activity for the entire species. The inference that all genotypes of the species (individuals or colonies) were antibacterially active would have been automatic—and wrong. The correctly replicated methods shows that, in the cited study, antibacterial activity could not be the only defense against bacterial epibiosis, because for each replicate extract between 20 and 100% of the local strains tested were insensitive. In situ, these strains would quickly colonize the ascidian, were it not for additional defenses-repellence in this case. Finally, these results illustrate that in-vitro activities against single target species should not be interpreted as general activities against whole multispecies colonizer groups (antibacterial, antilarval) which, in view of biological and physiological diversity within the colonizer pool, is not really surprising.

In conclusion, chemical antiepibiosis defenses seem to be widespread and common. To date, several thousand marine natural products have been isolated. A few seem to be of medical interest. Regrettably, the effort and success of the natural products chemists is not matched by chemical ecologists. Our understanding of chemical interactions, maybe the most important level of interactions in the sea, is still in an embryonic state.

Mechanical

• Microtopography: There are hints in the literature (Linskens 1966, Harlin and Lindbergh 1977, Halcrow and Bousfield 1987, Richmond and Seed 1991) that surface structure influences settlement behavior of bacteria spores and larvae. Some diatom species, too, exhibited selective settlement when offered plates coated with monolayers of glass beads with 0.1, 0.5, 1.0 and 5.0 mm diameter, respectively (personal observation). The study of Forsberg (1994) impressively illustrates the total inhibition of macrofouling by "hairy" surfaces (textile fibers attached vertically to plates). Many marine organisms possess surface microtopographies of great beauty and mysterious function. It might be rewarding to have a closer look at the defensive role of surface structure, possibly acting through available attachment area or microhydrodynamics.

• Mucous secretion: Establishment of an epibiotic community may be severely impaired by an increase of physical and/or temporal surface instability. This can be accomplished by continuous or sporadic mucous secretion leading to clogging of cilia and flagellae, reduced adhesion or physical removal of settlers when mucus dissolves or washes off. Surface mucous production is extremely widespread among marine animals and

algae (e.g., Fontaine 1964, Ducklow and Mitchell 1979, Krupp 1984 Dyrynda 1986, Thorp et al. 1991). Cilia-driven migrating mucous films are known from cnidarians and echinoderms (e.g., Barnes 1987).

• Sloughing: Sporadic, sacrificial surface renewal is called sloughing. In this process, the outermost surface of an organism is shed, together with most epibionts having settled since the previous sloughing event. This discarded layer may be cellular tissue or a cuticle. Many algae slough mucous cuticles (e.g., Sieburth and Tootle 1981, Moss 1982, Johnson and Scheibling 1987, Kaspar 1992, Martinez and Correa 1993) or epidermis layers (e.g., Russel and Veltkamp 1984, Filion-Myklebust and Norton 1986). Numerous sponges and cnidarians sporadically secrete and discard mucous layers (e.g., Coll et al. 1987, Targett 1988, Barthel and Wolfrath 1989). Similar sloughing behavior has been observed in serpulid polychaetes (Thorp et al. 1991), holothurians (personal observations), nematodes (Barnes 1987), didemnid ascidians (Wahl and Banaigs 1990). The significance of flaking for turtle epibionts has been reported (Matsuura and Nakamura 1993). Sloughing of hard cuticles, molting, is best known from crustaceans. While it works well as an epibiosis-reducing mechanism when molting frequency is high enough (e.g., every 4–7 days to inhibit diatom colonization; Allen et al. 1993), molting has certainly not evolved primarily as an antiepibiosis-defense adaptation: it normally is too infrequent, too costly, and too risky (Bauer 1989). Strictly speaking, sloughing does not inhibit colonization, but it interrupts the aufwuchs sequence. The sloughing frequency necessary to keep epibiosis at a tolerable level depends on the local colonizing pressure.

• Grooming: Numerous crustaceans possess cleaning appendages, the loss of which leads to an increase in epibiosis (Bauer 1989). Aquatic insect larvae may behave similarly, and caddis fly larvae have been observed cleaning the accessible parts of their case (Bergey and Resh 1994).

• Abrasion: The abrasive effect of sediment particles in regularly burrowing forms or inhabitants of the surf zone undoubtedly represents a severe stress for epibionts. Thus, burrowing behavior may have multiple benefits: shelter from turbulence, hiding from predators, avoiding pelagic settlers, shaving off already attached ones, and maybe searching for food.

Associational resistance: The presence of other organisms may contribute to a potential basibiont's resistance to epibiosis. Well defended epibionts have the potential to impede further colonization of the host. Antifoulant secreting bacteria on an ascidian (Kjelleberg and Holmstroem 1994) or antifungal bacteria on crustacean embryos (Gil-Turnes et al. 1989) are known examples, but other predominantly 'clean' epibionts like hydrozoans, bryozoans or sponges have the potential to play similar roles. In particular, encrusting epibionts on shells or carapaces could contribute to the overall defense of the association without too many detrimental effects.

Intra- and interspecific grooming remains to be mentioned. We have shown previously that mutual shell grazing between *Littorina littorea* individuals contributes substantially to the control of epibiosis (Wahl and Sönnichsen 1992). When this social grooming was impeded, the shells were colonized rapidly. Also, motile basibiont-associated predators, like diatom-feeding harpacticoids or fungi-eating acarida, may assist in controlling epibiosis (Wahl and Banaigs 1990). Repeatedly, grazing of epibiont has been found to increase fitness and productivity of the basibiont (e.g., Bulthuis and Woelkerling 1983, Cattaneo 1983, Howard and Short 1986). In some cases, basibionts even attract grazers or induce the settlement of their larvae (Bronmark 1985, Kaspar 1992).

Concluding, a wide spectrum of behavioral possibilities has evolved in the face of colonization pressure. There certainly is no best solution for everyone in any situation. It is probably the exception to find species relying on a single pattern. Most often, a combination of different strategies will be found: permanent versus temporary avoidance, or tolerance on body parts where epibiosis does not harm or during phases of inactivity, defense for the rest. Defense itself often is multiple: chemical plus sloughing plus grazing (didemnid ascidian: Wahl and Banaigs 1990), chemical plus unstable mucous surface (octocorals: Coll et al. 1987, Targett 1988), grooming plus nocturnal behavior plus burrowing (crustaceans: Bauer 1989), repellent activity plus antibiotic activity plus mucous secretion (ascidian: Wahl et al. 1994), and so on. The advantage of multiple defense systems (beside its broad-spectrum efficiency) is, that a pre-adaptation for insensitivity toward one defense is not rewarded by an immediate colonization success. Thus, coevolution by epibionts is more difficult than in a one-type defensive system. Could that be a reason for the scarcity of specialized and strict epibionts?

One selective advantage of evolving temporary, local or permanent tolerance toward epibiosis could be the saving of defense costs. It has not been decided yet whether defense in general is costly or not (e.g., Coley 1986, Larsson et al. 1986, Hay and Fenical 1988, Paul and Van Alstyne 1988, Fagerström 1989, Yates and Peckol 1993). Defense costs are the sum of (1) energy and nutrients consumed for defense production and, therefore, lost to growth, (2) energy necessary for sequestering toxins away from active cell processes, (3) interference of some defenses with photosynthesis, and (4) loss of productivity of the tissue that was not grown because of defense expenses (Coley 1986). On the other hand,

(e.g., Kearsley and Whitham 1992) or the defense could be a free by-effect of some different function (e.g., molting serves primarily growth; Bauer 1989). Finally, even if a specific defense system is costly, in habitats where food is not the limiting factor this may not matter much.

Antiepibiosis and Antifouling

Antifouling is the technology of inhibiting aufwuchs on man-made structures in the sea. Antiepibiosis is the multitude of defense systems developed by marine organisms to protect themselves or parts of themselves against aufwuchs. Antiepibiosis is at work since Precambrian times, protecting immersed surfaces, the sum of which is many orders of magnitude larger than all man-made structures taken together. Nevertheless, from antiepibiosis no environmental problems have arisen so far. Our clumsy attempts at ship hull protection during the last hundred years did that job thoroughly. Maybe we should not try to skip those one billion years of trial and error and gradual improvement, but instead try to tap the accumulated expertise.

Numerous authors have recommended to screen for natural antifoulants in marine organisms and incorporate these in appropriate paint matrices to replace the discredited TBT, copper, arsenic, etc. (e.g., Goto et al. 1992, Foster 1994, Holmstroem and Kjelleberg 1994, Railkin and Dobrestov, in press). There are several concerns about this approach:

- It would be unwise to repeat the old mistake to widely deploy new (at least in this function, this concentration or this part of the world) chemical defense systems before knowing exactly the toxicity of the compounds used and their long-term environmental impact (susceptibility of nontarget species, bioaccumulation, biomagnification, compound half-lifes, sediment enrichment).
- The chances of isolating single compounds that inhibit (or repel) the whole range of potential colonizers, from bacteria to chordates in all seas, are supposedly very small. As mentioned before, most organisms use multiple defense systems.
- The chances to find, by a more or less blind screening, complementarily active compounds, i.e., that are antibacterial, antidiatom, antilarval, antifungal, antialgal, respectively, and that are environmentally harmless, and of combining them in the right proportions without degrading interactions between them, and developing the right matrix with the right leaching rates, etc. are smaller still. Just look at the devastatingly low hit rate in marine pharmacology. This is not only due to the restrictive admission standard for new drugs, for similarly severe criteria will some day (soon hopefully) be used in environmental legislation.

An integral approach to the problem seems more promising.

Imitating Natural Defense Systems

In order to learn from evolution, we should try to understand the entire defense system used by a species to protect itself against epibiosis. For this, an interdisciplinary approach is necessary, including ecologists, biophysicists, organochemists, immunologists, and microbiologists. In a first step this would be fundamental research with the goal to, for once, understand a defense system in its integrity (and not by looking at a few isolated pieces). Then, and with a technological application in mind, the research should concentrate on such defense systems adaptable to human interests. It would be desirable to renounce the use of leaching chemicals (antifoulants and matrix polymers). Assessing the environmental impact of these (toxicity, mutability, accumulation, long-term effects) is extremely difficult and time-consuming. The future antifouling paints should be nonsacrificial, nonleaching, and strictly surface bound. In this regard, defensive subsystems like wettability, surface microtopography, surface-bound toxins or repellents, and substratum consistency are of particular interest. The chances to encounter defense systems (partly) transferable to marine technology may be increased by investigating adequate life forms. Criteria for selecting promising research objects might be:

- high antifouling potential index as presented in the section on "Colonization of an Immersed Substratum" (i.e., absence of epibiosis on nonephemerous substrata despite intense colonization pressure)
- considerable longevity of the organism and of its surface
- hard or tough surface
- absence of leaching chemical defense
- absence of other nontransferrable defense subsystem (extreme pH, mucous production, frequent or continuous sloughing, associated grazers, avoidance behavior, etc.). Promising research targets might be certain large crustaceans, sharks or some molluscan shells.

(e.g., Kearsley and Whitham 1992) or the defense could be a free by-effect of some different function (e.g., molting serves primarily growth; Bauer 1989). Finally, even if a specific defense system is costly, in habitats where food is not the limiting factor this may not matter much.

Antiepibiosis and Antifouling

Antifouling is the technology of inhibiting aufwuchs on man-made structures in the sea. Antiepibiosis is the multitude of defense systems developed by marine organisms to protect themselves or parts of themselves against aufwuchs. Antiepibiosis is at work since Precambrian times, protecting immersed surfaces, the sum of which is many orders of magnitude larger than all man-made structures taken together. Nevertheless, from antiepibiosis no environmental problems have arisen so far. Our clumsy attempts at ship hull protection during the last hundred years did that job thoroughly. Maybe we should not try to skip those one billion years of trial and error and gradual improvement, but instead try to tap the accumulated expertise.

Numerous authors have recommended to screen for natural antifoulants in marine organisms and incorporate these in appropriate paint matrices to replace the discredited TBT, copper, arsenic, etc. (e.g., Goto et al. 1992, Foster 1994, Holmstroem and Kjelleberg 1994, Railkin and Dobrestov, in press). There are several concerns about this approach:

- It would be unwise to repeat the old mistake to widely deploy new (at least in this function, this concentration or this part of the world) chemical defense systems before knowing exactly the toxicity of the compounds used and their long-term environmental impact (susceptibility of nontarget species, bioaccumulation, biomagnification, compound half-lifes, sediment enrichment).
- The chances of isolating single compounds that inhibit (or repel) the whole range of potential colonizers, from bacteria to chordates in all seas, are supposedly very small. As mentioned before, most organisms use multiple defense systems.
- The chances to find, by a more or less blind screening, complementarily active compounds, i.e., that are antibacterial, antidiatom, antilarval, antifungal, antialgal, respectively, and that are environmentally harmless, and of combining them in the right proportions without degrading interactions between them, and developing the right matrix with the right leaching rates, etc. are smaller still. Just look at the devastatingly low hit rate in marine pharmacology. This is not only due to the restrictive admission standard for new drugs, for similarly severe criteria will some day (soon hopefully) be used in environmental legislation.

An integral approach to the problem seems more promising.

Imitating Natural Defense Systems

In order to learn from evolution, we should try to understand the entire defense system used by a species to protect itself against epibiosis. For this, an interdisciplinary approach is necessary, including ecologists, biophysicists, organochemists, immunologists, and microbiologists. In a first step this would be fundamental research with the goal to, for once, understand a defense system in its integrity (and not by looking at a few isolated pieces). Then, and with a technological application in mind, the research should concentrate on such defense systems adaptable to human interests. It would be desirable to renounce the use of leaching chemicals (antifoulants and matrix polymers). Assessing the environmental impact of these (toxicity, mutability, accumulation, long-term effects) is extremely difficult and time-consuming. The future antifouling paints should be nonsacrificial, nonleaching, and strictly surface bound. In this regard, defensive subsystems like wettability, surface microtopography, surface-bound toxins or repellents, and substratum consistency are of particular interest. The chances to encounter defense systems (partly) transferable to marine technology may be increased by investigating adequate life forms. Criteria for selecting promising research objects might be:

- high antifouling potential index as presented in the section on "Colonization of an Immersed Substratum" (i.e., absence of epibiosis on nonephemerous substrata despite intense colonization pressure)
- considerable longevity of the organism and of its surface
- hard or tough surface
- absence of leaching chemical defense
- absence of other nontransferrable defense subsystem (extreme pH, mucous production, frequent or continuous sloughing, associated grazers, avoidance behavior, etc.). Promising research targets might be certain large crustaceans, sharks or some molluscan shells.

Living Surfaces

As mentioned before, well defended, encrusting epibionts are likely to inhibit further aufwuchs on the basibiont. Why not grow such organisms on ship hulls (already suggested by Goupil et al. 1973)? Possible candidates are bacteria, encrusting (noncalcareous) algae, sponges, and colonial ascidians. Among these phyla are numerous species that have perfectly clean, sometimes sterile, surfaces and might even contribute to frictional drag reduction by hydrophobic or smooth and soft surfaces. Growing and maintaining a monospecific culture of such a species on the hull certainly is a technological problem. Several suggestions come to mind:

- matrices with species-specific settlement cues
- preculture of hulls in settlement tanks
- incorporation of permanent, resting or artificially preserved dispersal stages (resting eggs, gemmules, spores, larvae) into the matrix that could ensure a permanent recolonization of the hull surface in case of damage
- biotechnological gene-manipulation of antifouling species to make it a superior competitor but exclusively on a specifically designed biomatrix.

This may sound like science fiction, but hopefully some day a really new antifouling technique will allow us to use the sea without simultaneously destroying it.

LITERATURE CITED

Abello, P., and E. Macpherson. 1992. Epibiosis and rhizocephalan infestation patterns in relation to the reproductive biology of *Lithodes ferox* (Filhol, 1885) (Anomura: Lithodidae). *J. Crust. Biol.* 12(4): 561–570.

Absolom, D.R., F.V. Lamberti, Z. Policova, W. Zingg, C.J. Vanoss, and A.W. Newmann. 1983. Surface thermodynamics of bacterial adhesion. *Appl. Environ. Microbiol.* 46(1): 90–97.

Allen, Y.C., B.T. De-Stasio, and C.W. Ramcharan. 1994. Individual and population level consequences of an algal epibiont on *Daphnia*. *Limnol. Oceanogr.* 38(3): 592–601.

Altena, I. Van, and A.J. Butler. 1994. Antifoulants from marine invertebrates. Pages 80–86 in S. Kjelleberg and P. Steinberg, eds. *Biofouling: Problems and Solutions.* University of New South Wales, Sydney.

Aroujo Jorge, T.C., C.M.L.M. Coutinho, and L.E.V. Aguiar. 1992. Sulphate reducing bacteria associated with biocorrosion: a review. *Mem. Inst. Oswaldo Cruz.* 87(3): 329–337.

Baier, R.E. 1981. Early events of microbiofouling of all heat transfer equipment. Pages 293–304 in E.F.C. Somerscules and J.G. Knudsen, eds. *Fouling of Heat Transfer Equipment.* Hemisphere Publ. Corp., Washington, D.C., New York, London.

Baier, R.E. 1984. Initial events in microbial film formation. Pages 57–62 in J.D. Costlow and R.C. Tipper, eds. *Marine Biodeterioration: An Interdisciplinary Study.* E.& F.N. Spon Ltd., London.

Baker, J.H., and D.R. Orr. 1986. Distribution of epiphytic bacteria on freshwater plants. *J. Ecol.* 74: 155–165.

Bakus, G.J., N.M. Targett, and B. Schulte. 1986. Chemical ecology of marine organisms: an overview. *J. Chem. Ecol.* 12(5): 951–987.

Ballentine, D.L. 1979. The distribution of algal epiphytes on macrophyte hosts offshore from La Parguera, Puerto Rico. *Bot. Mar.* 22: 107–111.

Barkai, A., and C. McQuaid. 1988. Predator-prey role reversal in a marine benthic ecosystem. *Science* 242: 62–64.

Barnes, R.D. 1987. *Invertebrate Zoology.* 5th Edition. Saunders College Publ., Philadelphia.

Barthel, D., and B. Wolfrath. 1989. Tissue sloughing in the sponge *Halichondria panicea:* a fouling organism prevents being fouled. *Oecologia* 78: 357–360.

Batley, G.E., J.C. Chapman, and S.P. Wilson. 1994. Environmental impact of antifouling technology. Pages 19–53 in S. Kjelleberg and P. Steinberg, eds. *Biofouling: Problems and Solutions.* University of New South Wales, Sydney.

Bauer, R.T. 1989. Decapod crustacean grooming: Functional morphology, adaptive value, and phylogenetic significance. Pages 49–73 in B.E. Flegenbauer, L. Watling, and A.B. Thistle, eds. *Function Morphology of Feeding and Grooming in Crustacea.* Balkema, Rotterdam.

Becker, K. 1994. Zur Bedeutung der Substratoberflächenspannung für die Verhinderung von Aufwuchs auf Belebten und unbelebten Substraten im Meer. Ph.D. Thesis, University of Kiel, Germany.

Becker, K., and M. Wahl. 1991. Influence of substratum surface tension on biofouling of artificial substrata in Kiel Bay (Western Baltic): in situ studies. *Biofouling* 4: 275–291.

Becker, K., and M. Wahl. 1996. Behavioural patterns as natural antifouling mechanisms of tropical marine crabs. *J. Exp. Mar. Biol. Ecol.* In press.

Bergey, E.A., and V.H. Resh. 1994. Interactions between a stream caddisfly and the algae on its case: factors affecting algal quantity. *Freshwater Biol.* 31: 153–163.

Bhosle, N.B., D. McCarrol, L.V. Evans, and R.G.J. Edyvean. 1993. Effects of cathodic polarisation on carbohydrate metabolism in *Amphora coffeaeformis*, a marine fouling diatom. *Biofouling* 7(3): 171–185.

Bloom, S.A. 1975. The motile escape response of a sessile prey: a sponge-scallop mutualism. *J. Exp. Mar. Biol. Ecol.* 17: 311–321.

Boudreau, B.E. Bourget, and Y. Simard. 1990. Benthic invertebrate larval responses to substrate characteristics at settlement: shelter preferences of the American lobster *Homarus americanus*. *Mar. Biol.* 106: 191–198.

Bowmer, C.T., and G. Ferrari 1989. A new approach to the development and testing of antifouling paints. *J. Oil Color Chem. Assoc.* 72(10): 391–396.

Boyle, P.J. 1988. Marine wood biodeterioration and wood-boring crustaceans. Pages 167–188 in M.F. Thompson, R. Sarojini, and R. Nagabushanam, eds. *Marine Biodeterioration.* Oxford & IBH Publishing Co. Pvt. Ltd., New Delhi and A.A. Balkema, Rotterdam.

Brönmark, C. 1985. Interactions between macrophytes, epiphytes and herbivores: an experimental approach. *Oikos* 45: 26–30.

Brooks, W.R. 1989. Hermit crabs alter sea anemone placement patterns for shell balance and reduced protection. *J. Exp. Mar. Biol. Ecol.* 132: 109–121.

Bulthuis, D.A., and W.J. Woelkerling. 1983. Biomass accumulation and shading effects of epiphytes on leaves of seagrass, *Heterozostera tasmanica*, in Victoria, Australia. *Aquat. Bot.* 16: 137–148.

Burke, R.D. 1986. Pheromones and the gregarious settlement of marine invertebrate larvae *Bull. Mar. Sci.* 39(2): 323–331.

Busscher, H.J. 1985. Surface free energies and the adhesion of oral bacteria. Ph.D. Thesis, Rijksuniversiteit te Groningen, NI.

Butman, C.A. 1986. Larval settlement of soft-sediment invertebrates: the spatial scales of pattern explained by active habitat selection and the emerging role of hydrodynamical processes. *Oceanogr. Mar. Biol. Ann. Rev.* 25: 113–165.

Caron, D.A., and J. Mcn. Sieburth, 1981. Disruption of the primary fouling sequence on fiber glass-reinforced plastic submerged in the marine environment. *Appl. Environ. Microbiol.* 41: 268–273.

Cattaneo, A. 1983. Grazing on epiphytes. *Limnol. Oceanogr.* 28: 124–132.

Chabot, R., and E. Bourget. 1988. Influence of substratum heterogeneity and settled barnacle density on the settlement of cypris larvae. *Mar. Biol.* 97: 45–56.

Characklis, W.G., and K.E. Cooksey. 1983. Biofilms and microbial fouling. *Adv. Microbial Fouling* 29: 93–138.

Characklis, W.G. 1981. Fouling biofilm development: a process analysis. *Biotechnol. Bioeng.* 23: 1923–1960.

Chet, I., and R. Mitchell. 1976. Ecological aspects of microbial chemotactic behavior. *Ann. Rev. Microbiol.* by *Ann. Rev. Inc.* 30: 221–239.

Chevolot, L., J.C. Cochard, and J.C. Yvin. 1991. Chemical induction of larval metamorphosis of pecten maximus with a note on the nature of naturally occurring triggering substances. *Mar. Ecol. Prog. Ser.* 74: 83–89.

Chiavelli, D.A., E.L. Mills, and S.t. Threlkeld. 1993. Host preference, seasonality, and community interactions of zooplankton epibionts. *Limnol. Oceanogr.* 38(3): 574–583.

Claisse, D., and C. Alzieu. 1993. Copper contamination as a result of antifouling paint regulations? *Mar. Pollution Bull.* 26(7): 395–397.

Clarkson, N., and L.V. Evans. 1993. Evaluation of a potential non-leaching biocide using the marine fouling diatom *Amphora coffeaeformis. Biofouling* 7(3): 187–195.

Coley, P.D. 1986. Costs and benefits of defense by tannins in a neotropical tree. *Oecologia* 70: 238–241.

Coll, J.C., I. R. Price, G.M. Konig, and B.F. Bowden. 1987. Algal overgrowth of alcyonacean soft corals. *Mar. Biol.* 96: 129–135.

Collinson, R., and C. Grant. 1994. An Australian shipping industry perspective. Pages 14–18 in S. Kjelleberg and P. Steinberg, eds. *Biofouling: Problems and Solutions.* University of New South Wales, Sydney.

Cooksey, B., K.E. Cooksey, C.A. Millar, J.H. Paul, R. Rubin, and D. Webster. 1984. The attachment of microfouling diatoms. Pages 167–172 in J.D. Costlow and R.C. Tipper, eds. *Marine Biodeterioration: An Interdisciplinary Study.* E. & F.N. Spon Ltd., London.

Cori, C.I. 1936. Kamptozoa. In H.G. Brouns, ed. *Klassen und Ordnungen des Tierreiches* Band 4(11,4), Akad. Verlagsges. Leipzig.

Corpe, W.A. 1972. Microfouling: the role of primary film forming marine bacteria. *International Congress on Marine Corrosion and Fouling.* National Bureau of Standards, Gaithersburg, Maryland.

Corpe, W.A. 1982. Microbial attachment and growth on solid surfaces. Pages 35–43 in *Chemical Disinfection: New Concepts and Materials.* New York.

Costerton, J.W., G.G. Geesey, and K.J. Cheng. 1978. How bacteria stick. *Sci. Am.* 238: 86–95.

Coutinho, C.M., F.C. Magalhaes, and T.C. Aroujo-Jorge. 1993. Scanning electron microscope study of biofilm formation at different flow rates over metal surfaces using sulphate-reducing bacteria. *Biofouling* 7: 19–27.

Crisp, D.J. 1972, Mechanisms of adhesion of fouling organisms. Pages in 691–699 in *International Congress on Marine Corrosion and Fouling.* National Bureau of Standards, Gaithersburg, Maryland.

Crisp, D.J. 1984. Overview of research on marine invertebrate. larvae. Pages 103–126 in J.D. Costlow, and R.C. Tipper, eds. *Marine Biodeterioration: An Interdisciplinary Study.* E. & F.N. Spon Ltd., London.

D'Antonio, C. 1985. Epiphytes on the rocky intertidal red alga *Rhodomela larix* (Turner) C. Agardh: Negative effects on the host and food for herbivores? *J. Exp. Mar. Biol. Ecol.* 86: 197–218.

Davies, I.M., and J.D. Paul. 1986. Accumulation of copper and nickel from antifouling compounds during cultivation of scallops (*Pecten maximus* L.) and Pacific oysters (*Crassostrea gigas* Thun.). *Aquaculture* 55: 93–102.

Davis, A.R., and A.E. Wright. 1989. Interspecific differences in fouling of two congeneric ascidians (*Eudistoma olivaceum* and *E. capsulatum*): is surface acidity an effective defense? *Mar. Biol.* 102: 491–497.

Davis, A.R., N.M. Targett, O.J. McConnell, and C.M. Young. 1989. Epibiosis of marine algae and benthic invertebrates: natural products chemistry and other mechanisms inhibiting settlement and overgrowth. Pages 86–114 in P.J. Scheuer, ed. *BioOrganic Marine Chemistry.* Vol. 3. Springer Verlag, Berlin, Heidelberg.

Dayton, P.K. 1971. Competition, disturbance and community organization: the provision and subsequent utilization of space in a rocky intertidal community. *Ecol. Monogr.* 41: 351–389.

De, C.B. 1989a. Antifouling paints—present constraints and future. *Paintindia* 39: 13–14.

De, C.P. 1989b. Toll of the sea—countdown for antifouling paints. *Paintindia* 39: 21–23.

Denny, M.W. 1988. *Biology and the Mechanics of the Wave-swept Environment.* Princeton University Press, Princeton, New Jersey.

DePalma, V.A., D.W. Goupil, and C.K. Akers. 1979. Field demonstration of rapid microfouling in model heat exchangers: Gulf of Mexico, Nov. 1978. *Proceedings 6th OTEC Conference.* Applied Physics Laboratory, John Hopkins University, Baltimore.

Dexter, S.C. 1993. Role of microfouling organisms in marine corrosion. *Biofouling* 7(2): 97–127.

Dexter, S.C. 1976. Influence of substrata wettability on the formation of bacterial slime films on solid surfaces immersed in natural seawater. Pages 137–144 in *Proceedings 4th International Congress on Marine Corrosion and Fouling,* Boulogne, France.

Dexter, S.C. 1978. Influence of substratum critical surface tension on bacterial adhesion—in-situ studies. *J. Coll. Interf. Sci.* 70: 346–354.

Dexter, S.C., and K.E. Lucas. 1985. The study of biofilm formation underwater by photoacoustic spectroscopy. *J. Coll. Interf. Sci.* 104(1): 15–27.

Dexter, S.C., and S.H. Lin. 1991. Effect of marine bacteria on calcareous deposition. *Mat. Perform.* 30(4): 16–21.

Dexter, S.C., J.D. Sullivan, Jr., J. William, III., and S.W. Watson. 1975. Influence of substrate wettability on the attachment of marine bacteria to various surfaces, *Appl. Microbiol.* 30(2): 298–308.

Dixon, J., S.C. Schroeter, and J. Kastendiek. 1981. Effects of encrusting bryozoan, *Membranipora membranacea;* on the loss of blades and fronds by the giant kelp, *Macrocystis pyrifera* (Laminariales). *J. Phycol.* 17: 341–345.

Ducklow, H..W., and R. Mitchell. 1979. Bacterial populations and adaptations in the mucous layers on living corals. *Limnol. Oceanogr.* 24(4): 715–725.

Durante, K.M., and F.S. Chia. 1991. Epiphytism on *Agarum fimbriatum:* can herbivore preferences explain distribution of epiphytic bryozoans? *Mar. Ecol. Prog. Ser.* 77: 297–287.

Dyrynda, P.E.J. 1986. Chemical defenses and the structure of subtidal epibenthic communities. Pages 411–424 in P.E. Gibbs, ed. *Proceedings 19th European Marine Biology Symposium.* Cambridge University Press, Cambridge.

Fagerstrom, T. 1989. Antiherbivory chemical defense in plants: a note on the concept of cost. *Am. Nat.* 133(2): 281–287.

Fattom, A., and M. Shilo. 1984. Hydrophobicity as an adhesion mechanism of benthic cyanobacteria. *Appl. Environ. Microbiol.* 47(1): 135–143.
Feifarek, B.P. 1987. Spines and epibionts as antipredator defenses in the thorny oyster *Spondylus americanus* Hermann. *J. Exp. Mar. Biol. Ecol.* 105: 39–56.
Ferreira, S., and U. Seeliger. 1985. The colonization process of algal epiphytes on *Ruppia maritima* L. *Bot. Mar.* 28: 245–249.
Filion-Myklebust, C., and T. A. Norton. 1986. Epidermis shedding in the brown seaweed *Ascophyllum nodosum* (L.) Le Jolis, and its ecological significance. *Mar. Biol. Lett.* 2: 45–51.
Fletcher, M., and S. McEldowney. 1984. Microbial attachment to nonbiological surfaces. Pages 124–129 in M.J. Klug and C.A. Reddy, eds. *Current Perspectives in Microbial Ecology.* Proceedings 3rd International Symposium on Microbial Ecology, Michigan State University.
Fletcher, R.L., and R.E. Baier. 1984. Influence of surface energy on the development of the green alga *Enteromorpha. Mar. Biol. Lett.* 5: 251–254.
Fontaine, A.R. 1964. The integumentory mucous secretions of the ophiuroid *Ophiocomina nigra. J. Mar. Biol. Assoc. UK* 44: 145–162.
Forsberg, G. 1994. Fiberflock—a biomimicking non-fouling concept. Pages 77–79 in S. Kjelleberg and P. Steinberg, eds. *Biofouling: Problems and Solutions.* University of New South Wales, Sydney.
Foster, A.C. 1994. Current antifouling technologies. Pages 44–48 in S. Kjelleberg and P. Steinberg, eds. *Biofouling: Problems and Solutions.* University of New South Wales, Sydney.
Fukagawa, T., and S. Suzuki. 1993. Cloning of gene responsible for tributyltin chloride (TBTCl) resistance in TBTCl-resistant marine bacterium, *Alteromonas* sp. M-1. *Biochem. Biophys. Res. Comm.* 194(2): 733–740.
Gaiser, E.E., and R.W. Bachmann. 1993. The ecology and taxonomy of epizoic diatoms on *Cladocera. Limnol. Oceanogr.* 38(3): 628–637.
Gaiser, E.E., and R.W. Bachman. 1994. Seasonality, substrate preference and attachment sites of epizoic diatoms on cladoceran zooplankton. *J. Plankton Res.* 16(1): 53–68.
Gaylord, B., C.A. Blanchette, and M.W. Denny. 1994. Mechanical consequences of size in wave-swept algae. *Ecol. Monogr.* 64(3): 28–313.
Gil-Turnes, M.S., M.E. Hay, and W. Fenical. 1989. Symbiotic marine bacteria chemically defend crustacean embryos from a pathogenic fungus. *Science* 246: 116–118.
Gocring, J.J., and P.L. Parker. 1972. Nitrogen fixation by epiphytes on seagrasses. *Limnol. Oceanogr.* 17(2): 320–323.
Goto, R., R. Kado, K. Muramoto, and H. Kamiya. 1993. Furospongolide, an antifouling substance from the marine sponge *Phyllaspongia papyracea* against the barnacle *Balanus amphitrite. Nippon Suisan Gakkaishi Bull. Jpn. Soc. Sci. Fish:* 59.
Goto, R., R. Kado, K. Muramoto, and H. Kamiya. 1992. Fatty acids as antifoulants in a marine sponge. *Biofouling* 6: 61–68.
Goupil, D.W., V.A. DePalma, and R.E. Baier. 1973. Prospects for nontoxic fouling resistant paints. Pages 445–458 in *Marine Industry: Problems and Opportunities.* Proceedings of the 9th Annual Conference of Marine Technology Society, Washington, D.C.
Griffith, J.R., and J.D. Bultman. 1980. Fouling release coatings. *Nav. Eng. J.* (1980): 129–132.
Hadfield, M.G. 1986. Settlement and recruitment of marine invertebrates: a perspective and some proposals. *Bull. Mar. Sci.* 39(2): 418–425.
Halcrow, K., and E. L. Bousfield. 1987. Scanning electron microscopy of surface microstructures of some gammaridean amphopod crustaceans. *J. Crust. Biol.* 7(2): 274–287.
Harlin, M.M. 1980. Seagrass epiphytes. Pages 117–151 in R.C. Phillips and C.P. McRoy, eds. *Handbook of Seagrass Biology: an Ecosystem Perspective.* Jerland STPM Press, New York.
Harlin, M.M., and J.M. Lindbergh. 1977. Selection of substrate by seaweeds: optimal surface relief. *Mar. Biol.* No: 33–40.

Hay, M.E. 1986. Associational plant defenses and the maintenance of species diversity: turning competitors into accomplices. *Am. Nat.* 128(5): 617–641.
Hay, M.E., and W. Fenical. 1988. Marine plant-herbivore interaction: the ecology of chemical defense. *Ann. Rev. Ecol. Syst.* 19: 111–145.
Henschel, J.R., and P.A. Cook. 1990. The development of a marine fouling community in relation to the primary film of microorganisms. *Biofouling* 2: 1–Nov.
Hodson, S.L., and C. Burke. 1994. Microfouling of salmon cage netting: a preliminary investigation. *Biofouling* 8: 93–105.
Holmstroem, C., and S. Kjelleberg. 1994. The effect of external biological factors on settlement of marine invertebrates and new antifouling technology. *Biofouling* 8: 147–160.
Horner, S.M.J. 1987. Similarity of epiphyte biomass distribution on *Posidonia* and artificial seagrass leaves. *Aquatic Bot.* 27: 159–167.
Howard, R.K., and F.T. Short. 1986. Seagrass growth and survivorship under the influence of epiphyte grazers. *Aquatic Bot.* 24: 287–302.
Jackson, J.B.C. 1977. Habitat area, colonisation and development of epifaunal community structure. Pages 349–358 in B.F. Keegan, P.O. Ceidigh, P.J.S. Boaden, eds. *Biology of Benthic Organisms.* Pergamon Press, London.
James, D.B. 1989. Boring and fouling echinoderms of Indian waters. Pages 227–238 in M.F. Thompson, R. Sarojini, and R. Nagabushanam, eds. *Marine Biodeterioration.* Oxford & IBH Publishing Co. Pvt. Ltd., New Delhi and A.A. Balkema, Rotterdam.
Johnson, C.R., D.G. Muir, and A.L. Reysenbach. 1991. Characteristic bacteria associated with surfaces of coralline algae: a hypothesis for bacterial induction of marine invertebrate larvae. *Mar. Ecol. Progr. Ser.* 74: 281–294.
Johnson, S.C., and R. E. Scheibling. 1987. Structure and dynamics of epifaunal assemblages on intertidal macroalgae *Ascophyllum nodosum* and *Fucus vesiculosus* in Nova Scotia, Canada. *Mar. Ecol. Progr. Ser.* 37: 209–227.
Kaspar, H.F. 1992. Oxygen conditions on surfaces of coralline red algae. *Mar. Ecol. Progr. Ser.* 81: 97–100.
Kearsley, M.J.C., and T.G., Witham. 1992. Guns and butter: a no-cost defense against predation for *Chrysomela confluens. Oecologia* 92: 556–562.
Keough, M.J. 1986. The distribution of a byrozoan on seagrass blades: settlement, growth and mortality. *Ecology* 67(4): 846–857.
Kirchman, D.L., and R. Mitchell. 1981. A biochemical mechanism for marine fouling. *Ocean* 7: 537–541.
Kirchman, D.L., D.L. Henry, and S.C. Dexter. 1989. Adsorption of proteins to surfaces in seawater. *Mar. Chem.* 27: 201–217.
Kitamura, H., and K. Hirayama. 1987. Effect of cultured diatom films on the settlement of larvae of a bryozoan *Bugula neritina. Nippon Suisan Gakkaishi* 53 (8): 1383–1385.
Kjelleberg, S.K., and C. Holmstroem. 1994. Antifoulants from bacteria. Pages 65–69 in S. Kjelleberg and P. Steinberg, eds. *Biofouling: Problems and Solutions.* University of New South Wales, Sydney.
Krupp, D.A. 1984. Mucus production by coral exposed during an extreme low tide. *Pac. Sci.* 38(1): 1–Nov.
Lailhonen, P., and E.R. Furman. 1986. The site of settlement indicates commensalism between blue mussel and its epibiont. *Oecologia* 71: 38–40.
Larsson, S., A. Wiren, L. Lundgrent, and T. Ericsson. 1986. Effects of light and nutrient stress on leaf phenolic chemistry in *Salix dasyclados* and susceptibility to *Galerucella lineola* (Coleoptera). *Oikos* 47: 205–210.
Leitz, T., and T. Wagner. 1993. The marine bacterium *Alteromonas epejiana* induces metamorphosis of the hydroid *Hydractinia echinata. Mar. Biol.* 115: 173–178.
Lesser, M.P., S.E. Shumway, T. Cucci, and J. Smith. 1992. Impact of fouling organisms on mussel rope culture: interspecific competition for food among suspension-feeding invertebrates. *J. Exp. Mar. Biol. Ecol.* 165: 91–102.

Lewis, J.A. 1994. Biofouling and fouling protection: a defensive perspective, Pages 39–43 in S. Kjelleberg and P. Steinberg, eds. *Biofouling: Problems and Solutions.* University of New South Wales, Sydney.

Lewis, T. 1994. Impact of biofouling on the aquatic industry. Pages 32–38 in S. Kjelleberg and P. Steinberg, eds. *Biofouling: Problems and Solutions.* University of New South Wales, Sydney.

Lining, T., and D.J. Garbary. 1992. The *Ascophyllum Polysiphonia Mycospaerella* symbiosis. *Bot. Mar* 35: 341–349.

Linskens, H.F. 1966. Oberflaechenspannung an marinen algen. *Proc. Kon. Ned. Akad. Wet.,* C. 66: 205–217.

Little, B.J. 1984. Succession in microfouling, Pages 63–67 in J.D. Costlow, R.C. Tipper, eds. *Marine Biodeterioration: An Interdisciplinary Study.* E. & F.N. Spon Ltd., London.

Little, B.J. 1985. Factors influencing the adsorption of dissolved organic material from natural waters. *J. Coll. Interf. Sci.* 108(2): 331–340.

Lynch, J.M., M. Fletcher, and M.J. Latham. 1979. Biological interactions. Pages 171–187 in J.M. Lynch, and N.J. Poole, eds. *Microbial Ecology: A Conceptual Approach.* Blackwell Science Publications.

Maki, J.S., D. Rittschof, J.D. Costlow, and R. Mitchell. 1988. Inhibition of attachment of larval barnacles, *Balanus amphitrite,* by bacterial films. *Mar. Biol.* 97: 199–206.

Marbach, A., and M. Tsurnamal. 1973. On the biology of *Berthellina citrina* (Gastropoda: Opisthobranchia) and its defensive acid secretion. *Mar. Biol.* 21: 331–339.

Marotz, G.W. 1985. Head losses ion intake pipes of desalination and power caused by mussel incrustation, and methods of prevention. Pages 180–184 in *Proceedings of the 21st IAHR Congress.* Melbourne, Australia.

Marshall, K.C. 1972. Mechanisms of adhesion of marine bacteria to surfaces. Pages 625–632 in *Proceedings 3rd International Congress on Marine Corrosion and Fouling.* National Bureau of Standards, Gaithersburg, Maryland.

Marshall, K.C. 1994. Biofouling—What's the problem? In S. Kjelleberg and P. Steinberg, eds. *Biofouling: Problems and Solutions.* University Of New South Wales, Sydney.

Marshall, K.C., R. Stout, and R. Mitchell. 1971. Mechanisms of the initial events in the sorption of marine bacteria to surfaces. *J. Gen. Microbiol.* 68: 337–348.

Martinez, E., and J.A. Correa. 1993. Sorus - specific epiphytism affecting the kelps *Lessonia nigrescens* and *L. trabeculata* (Phaeophyta). *Mar. Ecol. Progr. Ser.* 96: 83–93.

Matsuura, I., and K. Nakamura. 1993. Attachment pattern of the turtle barnacle *Chelonibia testudinaria* on carapace of nesting loggerhead turtle *Caretta caretta. Nippon Suisan Gakkaishi Bull. Jpn. Soc. Sci. Fish:* 59.

Mazure, H.G.F., and J.G. Field. 1980. Density and ecological importance of bacteria on kelp fronds in an upwelling region. *J. Exp. Mar. Biol. Ecol.* 43: 176–182.

McClintock, J.B., and J. Janssen. 1990. Pteropod abduction as a chemical defence in a pelagic Antarctic amphipod. *Nature* 346: 462–464.

Mebs, D. 1985. Chemical defense of a dorid nudibranch, *Glossidoris quadricolor* from the Red Sea. *J. Chem. Ecol.* 11(6).

Mitchell, R., and D. Kirchman. 1984. The microbial ecology of marine surfaces. Pages 49–58 in J.D. Costlow, and R.C. Tipper, eds. *Marine Biodeterioration: An Interdisciplinary Study.* E. & F.N. Spon, Ltd., London.

Mizobuchi, S., N. Shimidzu, M. Katsuoka, and K. Adachi. 1993. Antifouling substances against the mussel in an octocoral *Dendronephthya* sp. *NipponSuisan Gakkaishi Bull. Jpn. Soc. Sci. Fish* 59.

Monniot, C. 1961. Role of algae in the recruitment of marine invertebrate larvae. Pages 385–403 in D.M. John, S.J. Hawkins, and J.H. Price, eds. *Plant-Animal Interactions in the Marine Benthos.* Systematics Association, Clarendon Press, Oxford.

Morse, A.N.C. 1992. Role of algae in the recruitment of marine invertebrate larvae. Pages 385–403 in J.M. John, S.K. Hawkins, and J.H. Price, eds. *Plant-Animal interactions in the Marine Benthos.* Clarendon Press, Oxford.

Morse, D.E. 1984. Biochemical control of larval recruitment and marine fouling. Pages 137–140 in J.D. Costlow, and R.C. Tipper, eds. *Marine Biodeterioration: an Interdisciplinary Study.* E.&F.N. Spon Ltd., London.

Moss, B.L. 1982. The control of epiphytes by *Halidrys siliquosa* (L.) Lyngb. (Phaeophyta, Cystoseiraceae). *Phycologia* 21 (2): 185–191.

Nagabushanam, R., and S.M. Alam. 1988. An overview of research on marine biodeterioration in Indian waters, Pages 13–32 in M.F. Thompson and R. Nagabhushanam, eds. *Marine Biodeterioration.* Oxford & IBH Publishing Co. Pvt. Ltd., New Delhi and A.A. Balkema, Rotterdam.

Neumann, R. 1979. Bacterial induction of settlement and metamorphosis in the planula larvae of *Cassiopea andromeda* (Cnidaria: Scyphozoa, Rhizostomeae). *Mar. Ecol. Prog. Ser.* 1: 21–28.

O'Neill, T.B., and G.L. Wilcox. 1971. The formation of a primary film on material submerged in the sea at Port Hueneme, California. *Pac. Sci.* 25: 1–12.

Olson, R.R. 1980. Sun-shade adaptations of a colonial ascidian with a prokaryotic symbiont. *Am. Zool.* 20: 778.

Osman, R.W. 1977. The establishment and development of a marine epifaunal community. *Ecol. Monogr.* 47: 37–63.

Otero-Schmitt, J. and Sanjuan. 1992. Epibiotic seaweeds of the Cape Verde Islands. *Bot. Mar.* 35(5): 379–390.

Parry, D.L. 1984. Chemical properties of the test of ascidians in relation to predation. *Mar. Ecol. Progr. Ser.* 17: 279–282.

Patil, B.T., M.R. Gajendrachad, G. Ranganna, and T. Ramchandran. 1988. Effects of biofouling and corrosion on concrete structures. Pages 715–721 in M.F. Thompson and R. Nagabhushanam eds. *Marine Biodeterioration.* Oxford & IBH Publishing Co. Pvt. Ltd., New Delhi and A.A. Balkema, Rotterdam.

Paul, J.H., M.F. Defluan, and W.H. Jeffrey. 1986. Elevated levels of microbial activity in the coral surface layer. *Mar. Ecol. Progr. Ser.* 33: 29–40.

Paul, V.J. 1992. Chemical defenses of benthic marine invertebrates, Pages 164–188 in V.J. Paul, ed. *Ecological Roles of Marine Natural Products.* Comstock Publishing Assoc., Ithaca, New York.

Paul, V.J., and K.L. Van Alstyne. 1988. Chemical defense and chemical variation in some tropical Pacific species of *Halimeda* (Halimedaceae, Chlorophyta). *Coral Reefs* 6: 263–269.

Pawlik, J.R., and C. A. Butman. 1993. Settlement of a marine tubeworm as a function of current velocity: interacting effects of hydrodynamics and behavior. *Limnol. Oceanogr.* 38(8): 1730–1740.

Pearce, F. 1994. Offshore petroleum. Pages 19–31, S. Kjelleberg and P. Steinberg, eds., *Biofouling: Problems and Solutions.* University of New South Wales, Sydney.

Penhale, P.A. 1977. Macrophyte-epiphyte biomass and productivity in an eelgrass (*Zostera marine L.*) community. *J. Exp. Mar. Biol. Ecol.* 26: 211–224.

Peterson, S.M., G.E. Batley, and M.S. Scammell. 1993. Tetracycline in antifouling paints. *Mar. Pollut. Bull.* 26(2): 96–100.

Polz, M.F., Felbeck, R. Novak, M. Nebelsick, and J.A. Ott. 1992. Chemoautotrophic, sulfur-oxidizing symbiotic bacteria on marine nematodes: Morphological and biochemical characterization. *Microbial. Ecol.* 24(3): 313–329.

Precht, H. 1935. Epizoen der Kieler Bucht. Dissertation, University of Kiel.

Pringle, J.H., and M. Fletcher. 1983. Influence of substratum wettability on attachment of freshwater bacteria to solid surface. *Appl. Environ. Mivobiol.* 45(3): 811–817.

Rajaguru, A., and G. Shanta. 1992. Association between the sessile barnacle *Xenobalanus globicipites* (Coronulidae) and the bottlenose dolphin *Torsiops truncatus* (Delphinidae) from the Bay of Bengal, India, with a summary of previous records from cetaceans. *Fish. Bull.* 90: 197–202.

Rao, M.V., C.J. Cherian, and P.V. Cheriyan. 1991. Performance of 18m fender piles protected by scupper nailing in Cochin harbour waters. *J. Timber Dev. Assoc. (India)* 27(1): 33–37.

Richmond, C.A., and R. Seed. 1991. A review of marine macrofouling communities with special reference to animal fouling. *Biofouling* 3: 151–168.

Ridgway, H.F., M.G. Rigby, and D.G. Argo. 1985. Bacterial adhesion and fouling of reverse osmosis membranes. *J. Am. Water-work Assoc.* 77: 97–106.

Rittschof, D., E.S. Branscomb, and J.D. Costlow. 1984. Settlement and behavior to flow and surface in larval branacles, *Balanus amphitrite* Darwin. *J. Exp. Mar. Biol. Ecol.* 82: 131–146.

Roberts, D., D. Rittschof, E. Holm, and A.R. Schmidt. 1991. Factors influencing initial larval settlement: temporal, spatial and surface molecular components. *J. Exp. Mar. Biol. Ecol.* 150: 203–211.

Rosowski, J.R. 1992. Specificity of bacterial attachment sites on the filamentous diatom *Navicula confervacea* (Bacillariophyceae). *Can. J. Microbiol.* 38: 676–686.

Russell, F.E. 1984. Marine toxins and venomous and poisonous marine plants and animals (invertebrates). *Adv. Mar. Biol.* 21: 59–233.

Russell, G., and V.J. Veltkamp. 1984. Epiphyte survival on skin-shedding macrophytes. *Mar. Ecol. Progr. Ser.* 18: 149–153.

Sand-Jensen, K. 1977. Effect of epiphytes on eelgrass photosynthesis. *Aquat. Bot.* 3: 55–63.

Santhakumaran, J.N., and T.S.S. Rao. 1988. Observations on the destruction of timber by marine borers along the Goa coast. Pages 633–641 in M.F. Thompson, R. Sarojini and R. Nagabushanam, eds. *Marine Biodeterioration.* Oxford & IBH Publishing Co. Pvt. Ltd., New Delhi and A.A. Balkema, Rotterdam.

Sar, J., and E. Rosenberg. 1987. Fish skin bacteria: colonial and cellular hydrophobicity. *Microb. Ecol.* 13: 193–202.

Saroyan, J.R. 1968. Marine biology in antifouling paints. *J. Paint Technol.* 41(531): 285–303.

Schmitt, T.M. 1991. Chemical defense against fouling in the brown alga *Dictyota menstrualis.* Master's Thesis, Chapel Hill.

Schneider, R.P. 1994. Microbial biofilms. Pages 58–64 in S. Kjelleberg and P. Steinberg, eds. *Biofouling: Problem and Solutions.* University of New South Wales, Sydney.

Shibata, J., M. Kimura, K. Ueda, and Y. Seike. 1972. Ship hull anti-fouling system utilizing electrolized seawater. Pages 964–994 in *Proceedings 3rd International Congress on Marine Corrosion and Fouling,* National Bureau of Standards, Gaithersburg, Maryland.

Shimidzu, M., S. Katsuoka, K. Ina, S. Mizobuchi, and W. Miki. 1993. Isolation of betabisabolena as a repellent substance against blue mussel from an octocoral *Sinularis* sp. *Nippon-Suisan Gakkaishi Bull. Jpn. Soc. Sci. Fish:* 59.

Sieburth, J. Mcn., and J.L. Tootle. 1981. Seasonality of microbial fouling on *Ascophyllum nodosum* (L.) Lejol, *Fucus vesiculosus* L., *Polysiphonia lanosa* (L.) Tandy and *Chondrus crispus* Stackh. *J. Phycol.* 17: 57–64.

Steinberg, P.D., and R. De Nys. 1994. Natural antifoulants from seaweeds. Pages 70–76 in S. Kjelleberg and P. Steinberg, eds. *Biofouling: Problems and Solutions.* University of New South Wales, Sydney.

Stoecker, D. 1978. Resistance of a tunicate to fouling. *Biol.Bull.* 155: 615–626.

Sutherland, J.P. 1974. Multiple stable points in natural communities. *Am.Nat.* 108: 859–873.

Sutherland, J.P., and R.H. Karlson. 1977. Development and stability of the fouling community at Beaufort, North Carolina. *Ecol. Monogr.* 47: 425–446.

Targett, N.M. 1988. Allelochemistry in marine organisms: Chemical fouling and antifouling strategies. Pages 609–617 in M.F. Thompson, R. Sarojini, and R. Nagabushanam, eds. *Marine Biodeterioration.* Oxford & IBH Publishing Co. Pvt. Ltd., New Delhi and A.A. Balkema, Rotterdam.

Taylor, P.D., P.J. Schembri, and P. L. Cook. 1989. Symbiotic association between hermit crabs and bryozoans from the Otago region, southeastern New Zealand. *J. Nat. Hist.* 23: 1059–1085.

Thelin, I., and A.L. Bedhomme. 1983. Biomass des epiphytes des feuilles de *Posidonia oceanica* dans un herbier superficiel. *Rapp. Comm. Int. Mer Medit.* 28(3): 125–126.

Thorp, C.H., F.M. Sewell, and P.R. Bond. 1991. A self-cleaning mechanism in the operculum of *Serpula vermicularis* L. (Polychaeta: Serpulidae). *Bull. Mar. Sci.* 48(2): 412–419.

Threlkeld, S.T., D.A. Chiavelli, and R.L. Willey. 1993. The organization of zooplankton epibiont communities. *Trends Ecol. Evol.* 8(9) 317–321.

Threlkeld, S.T., and R.L. Willey. 1993. Colonization, interaction, and organization of cladoceran epibiont communities. *Limnol. Oceanogr.* 38(3): 584–591.

Todd, C.D., and R.W. Doyle. 1981. Reproductive strategies of marine benthic invertebrates: a settlement timing hypothesis. *Mar. Ecol.Progr. Ser.* 4: 75–83.

Tosteson, T.R., R. Revuelta, B.R. Zaidi, S.H. Imam, and R.F. Bard. 1983. Aggregation-adhesion enhancing macromolecules and the specificity of marine microbiol interactions. *J. Coll. Interf. Sci.* 104(1): 60–71.

Vogel, S. 1981. *Life in Moving Fluids.* Princeton University Press, Princeton, New Jersey.

Vogel, S. 1988. *Life's Devices.* Princeton University Press, Princeton, New Jersey.

Vrolijk, N.H., N.M. Targett, K.E. Baier, and A.E. Meyer. 1990. Surface characterisation of two gorgonian coral species: implications for a natural antifouling defense. *Biofouling* 2: 39–54.

Wahl, M. 1989. Marine epibiosis. I. Fouling and antifouling: some basic aspects. *Mar. Ecol. Progr. Ser.* 58: 175–189.

Wahl, M., and B. Banaigs. 1991. Marine epibiosis. III. Possible antifouling defense adaptation in *Polysyncraton lacazei* (Didemnidae, Ascidiacea). *J. Exp. Mar Biol. Ecol.* 145: 49–63.

Wahl, M., and M.E. Hay. 1995. Associational resistance and shared doom: Effect of epibiosis on herbivory. *Oecologia* 102: 329–340.

Wahl, M., and F. Lafargue. 1990. Marine epibiosis. II. Reduced fouling on *Polysycraton lacazei* (Didemnidae, Tunicata) and proposal of an antifouling potential index. *Oecologia* 82: 275–282.

Wahl, M., P.R. Jensen, and W. Fenical. 1994. Chemical control of bacterial epibiosis on ascidians. *Mar. Ecol. Progr. Ser.* 110: 45–57.

Wahl, M., and Sönnichsen. 1992. Marine epibiosis. IV. The periwinkle *Littorina littorea* lacks typical antifouling defences—why are some populations so little fouled? *Mar. Ecol. Prog. Ser.* 88(2-3): 225–235.

Wallis, R.C., and K.R. Strudwick. 1990. Nontoxic marine fouling release coatings. *Surface Coatings Australia* March 1990: 14–17.

Wardell, J.N., C.M. Brown, and B. Flannigan. 1983. Microbes and surfaces. Pages 350–378 in J.H. Slater, R. Whittenbury, and J.W.T. Wimpenny, eds. *Microbes in Their Natural Environment.* Cambridge University Press, Cambridge.

Weis, P., J.S. Weis, and E. Lores. 1993. Uptake of metals from chromated-copper-arsenate (CCA)-treated lumber by epibiota. *Mar. Pollution Bull.* 26(8): 428–430.

Wethey, D.S. 1986. Ranking of settlement cues by barnacle larvae: influence of surface contour. *Bull. Mar. Sci.* 39(2): 393–400.

Witman, J.D., and T.H. Suchanek. 1984. Mussels in flow: drag and dislodgement by epizoans. *Mar. Ecol. Progr. Ser.* 16: 259–268.

Yates, J.L., and P. Peckol. 1993. Effects of nutrient availability and herbivory on polyphenolics in the seaweed *Fucus vesiculosus. Ecology* 74(6): 1757–1766.